

For Reference

NOT TO BE TAKEN FROM THIS ROOM

For Reference

NOT TO BE TAKEN FROM THIS ROOM

Ex LIBRIS
UNIVERSITATIS
ALBERTAENSIS





Digitized by the Internet Archive
in 2018 with funding from
University of Alberta Libraries

<https://archive.org/details/Ransom1964>

#66
THE UNIVERSITY OF ALBERTA

REPRODUCTIVE BIOLOGY
OF WHITE-TAILED DEER IN MANITOBA

by

ALAN BRIAN RANSOM

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

APRIL, 1964

ABSTRACT

This study of reproductive biology of white-tailed deer (Odocoileus virginianus) is based on a sample of 159 does collected in Manitoba from three areas of different habitat quality during the winters of 1961, 1962 and 1963. The age of each fetus was determined by the growth curve method and the time of breeding was calculated by back-dating the assigned age from date of death. Ovaries were examined macroscopically to count corpora lutea of pregnancy. Inter-area comparisons are based on fawn, yearling and adult age classes as determined by tooth eruption. Incremental layers in the dental cement were used to determine chronological age for use in comparing fertility to age. Physical condition of deer collected in 1963 was assessed by means of kidney fat and femur marrow fat.

The peak of breeding activity occurred in November but was significantly earlier in the eastern area than in either the southerly or northerly area. Neither a difference in photoperiod nor autumn temperatures provides a satisfactory explanation. It is suggested that genetic or nutritional factors were responsible.

Fertility of adult does from all three study areas compared favourably with that of deer from other areas of North America. Fawn and yearling (except one area) fertility appeared to be relatively low compared with that of the adults. Ova loss rates for adults were 12.0, 4.5 and 1.5 percent and were apparently related to habitat quality. The large percentage ova loss for does from high quality range (12.0 percent) is attributed to a high frequency of triple ovulations that may have resulted from range conditions analogous

to "flushing". Fetal rates and their standard errors for adult does from each of the three areas, in order of decreasing habitat quality, were $1.92 \pm .09$, $1.92 \pm .10$ and $1.89 \pm .07$. Yearlings averaged $1.71 \pm .25$, $1.29 \pm .18$ and $1.11 \pm .11$. Fawns averaged $1.25 \pm .25$, $1.00 \pm .00$ and 0.0. Low yearling fertility is attributed primarily to high environmental resistance during the winter. Low quality summer range may be responsible for the absence of fawn breeding in one area. Fertility of adult does was not significantly affected by age but yearling fertility was significantly lower than that of adults thus showing the need for considering reproductive performance of yearlings separately from adult deer. It was found that fertility can vary significantly from year to year in response to environmental conditions. In this study fertility appeared to have been lowered during 1 year by extreme drought.

Condition of deer from all study areas decreased at approximately equal rates until many deer were suffering from malnutrition by late winter. It is suggested that under these circumstances survival of newborn fawns would depend largely on how fast spring range conditions allowed pregnant deer to regain weight.

A general comparison of environment is made between one study area (closed to hunting) and the Lake States of Minnesota, Wisconsin and Michigan. The conclusion is reached that lighter snowfall in Manitoba allows deer to cover a greater part of their summer range in winter than do Lake States deer, but that lower temperatures in Manitoba cause serious condition losses despite the availability of food. It is suggested that under such conditions the environmental resistance is sufficient to prevent deer irruptions in Manitoba and to hold maximum deer density far below that reached in the Lake States.

ACKNOWLEDGMENTS

The permission granted by Mr. G. W. Malaher, Director of the Manitoba Wildlife Branch, Department of Mines and Natural Resources, to use the information contained in this thesis is gratefully acknowledged. Most of the field and laboratory work on this study was carried out while I was employed by the Wildlife Branch. My year on campus was supported by the Civil Service Commission of the Manitoba Government.

Sincere gratitude is expressed to Mr. Eugene F. Bossenmaier, Chief of Game and Fur Management, Manitoba Wildlife Branch, for suggesting the study initially, for his continued advice and encouragement and for his helpful criticisms of this manuscript.

Special thanks are extended to Conservation Officers J. E. Bell, C. K. Brook, R. A. Cockle, R. Gilmore, H. Johnson, G. W. Medd and T. R. Rudolph for their many days of untiring field work performed largely under adverse field conditions. I also thank them for the hospitality extended to me while in the field.

Appreciation is also expressed to those Conservation Officers who gave of their time to assist those mentioned above.

For their help with field collections and laboratory work, sincere thanks are extended to H. D. Carr, H. D. Goulden, R. C. Goulden, R. E. McWhorter and R. J. Robertson, all of whom are past or present employees of the Manitoba Wildlife Branch.

Sincere appreciation is extended to Dr. W. A. Fuller and to Dr. J. C. Holmes, Zoology Department, University of Alberta, for their guidance during the final year of the study and for their criticisms of this manuscript.

Appreciation is expressed to Mr. Brian McPherson, now with the Department of Mathematics, University of Newfoundland, for his advice on statistical analysis of the data.

Thanks are also extended to Dr. K. L. Blaxter of the Hannah Dairy Research Institute, Scotland; to Dr. W. G. E. Evans of the Department of Entomology, University of Alberta; and to Mr. J. G. Stelfox of the Alberta Fish and Wildlife Branch, for their helpful comments on the manuscript.

Lastly, to my wife Judy, for her encouragement and for typing many drafts, sincere gratitude is expressed.

TABLE OF CONTENTS

INTRODUCTION	1
DEFINITION OF TERMS.	2
LITERATURE REVIEW.	5
DESCRIPTION OF STUDY AREAS	9
Whiteshell	9
Turtle Mountain.	10
Duck Mountain.	11
Comparison of Habitat Quality.	12
MATERIALS.	13
METHODS.	16
Field Collections.	16
Handling of Materials.	17
Age Determination.	17
Fetuses.	17
Fawns, yearlings and adults.	20
Ovary Examinations	21
Determination of Physical Condition.	21
Statistical Treatment of Data.	22
RESULTS.	24
Breeding Season.	24
Fawning Season	24
Ovulation Rates.	26
Ova Losses	26
Fetal Rates.	29
Yearly Variation in Ovulation and Fetal Rates.	29

Pregnancy Rates	32
Prenatal Mortality.	32
Size.	32
Physical Condition.	32
Sex Ratios of Fetuses	34
Reproductive Anomalies.	34
DISCUSSION.	39
Breeding Chronology	39
Latitudinal climatic factors.	40
Genetic factors	41
Nutritional factors	41
Theoretical Effects of Photoperiod and Temperature in	
Northern Areas.	42
Influence of Hunting on Breeding.	43
Influence of Range Quality on Ovulation and Ova Loss.	44
Influence of Age on Ovulation and Fetal Rates	47
Yearlings Versus Fawns as Indicators of Range Condition	47
Prenatal Mortality.	48
Breeding Among Female Fawns	49
Significance of Condition Data.	51
Fertility	52
Interpretation of Results	55
Weather	56
Food.	57
Other animals and other organisms causing disease	59
A place in which to live.	60

Concluding Statements.	61
RECOMMENDATIONS.	65
SUMMARY.	66
LITERATURE CITED	70

LIST OF TABLES

Table 1.	Place of origin and age composition of female white-tailed deer collected during the winters of 1961, 1962 and 1963.	15
Table 2.	Calculated breeding and fawning dates of female white-tailed deer from three areas of Manitoba.	25
Table 3.	Ovulation rates by age groups and area for white-tailed deer in Manitoba.	27
Table 4.	Fetal rates by age group and area for white-tailed deer in Manitoba	30
Table 5.	Mean yearly ovulation and fetal rates of adult white-tailed deer from three areas of Manitoba.	31
Table 6.	Sex ratios of white-tailed deer fetuses from three areas of Manitoba	38
Table 7.	Regional variations in pregnancy rates of white-tailed deer fawns.	50
Table 8.	Fertility of white-tailed deer from Manitoba compared to highest fertility levels reported from the United States. . .	53

LIST OF FIGURES

- Fig. 1. Outline map of Manitoba showing approximate centers of study areas, northern limit of white-tailed deer (dotted line) and northern limit of huntable populations (broken line) 8
- Fig. 2. Ova loss rates for three age groups of white-tailed deer from three areas of Manitoba (numbers of ova shed are shown in parentheses) 28
- Fig. 3. Pregnancy rates of white-tailed deer from three areas of Manitoba (sample size shown in parentheses) 33
- Fig. 4. Scatter diagram of kidney fat indices of yearling and adult white-tailed deer from three areas of Manitoba, plotted against time. 36
- Fig. 5. Scatter diagram of kidney fat indices plotted against percentage femur marrow fat of 34 deer from Manitoba. 37
- Fig. 6. Percentage of ova lost relative to number shed per Turtle Mountain adult white-tailed doe (numbers of ova shed are shown in parentheses) 46
- Fig. 7. Average monthly temperatures for Winnipeg (near Whiteshell) Manitoba and Chatham (near Cusino) Michigan 58

INTRODUCTION

White-tailed deer (Odocoileus virginianus) are numerically the most important big game animals hunted for sport in Manitoba. In recent years deer hunting has been increasingly popular but deer habitat has been diminishing through the expansion of the grain and livestock industries and through natural forest succession.

Until very recently most principles underlying deer management in Manitoba had been adopted from the United States but game managers realized that this practice was not necessarily sound since very little was known about the reproductive biology of white-tailed deer near the northern extremity of their range. Increasing necessity for more efficient management prompted the Manitoba Wildlife Branch to undertake a study, in 1960, of reproductive biology of white-tailed deer in three widely separated areas of the Province. The objectives called for a determination of breeding and fawning seasons, pregnancy rates, ovulation rates, fetal rates and prenatal losses. This thesis reports on the completed study.

DEFINITION OF TERMS

The following terms are defined to facilitate understanding of the text:

Corpus luteum of pregnancy

Ovulation in white-tailed deer apparently takes place at the end of the heat period or shortly thereafter. During ovulation the ovary wall ruptures and an ovum is shed. Following this the follicle collapses somewhat to allow repair of the rupture site. The follicular epithelial cells lining the follicle then enlarge greatly under the stimulus of luteinizing hormone to become granulosa lutein cells. These enlarged cells also become vacuolated and accumulate fatty material and lutein pigment which impart a yellow color to the granulosa cells. The aggregate of these cells is known as the corpus luteum of estrus or "yellow body". The corpus luteum of estrus functions as an endocrine gland and produces the hormone progesterone which inhibits further ovulation. It is maintained for approximately 14 to 15 days (Cheatum 1949a) under the influence of luteinizing hormone produced by the pituitary gland. If the shed ovum is not fertilized the corpus luteum of estrus degenerates. If it is fertilized the corpus luteum is maintained to parturition under the influence of chorionic gonadotrophin produced by the placenta and is then called a corpus luteum of pregnancy. Corpora are readily recognized in ovaries from pregnant deer. In cross section they appear as yellowish structures, usually 6 to 9 mm in diameter but extremes range from 3 to 13 mm (Haugen and Trauger 1962).

If two ova are shed during the cycle and only one is fertilized, both

corpora lutea will be maintained during pregnancy regardless of whether the ova were shed by one ovary or both.

Ovulation rate

The average number of ova shed per doe in the estrous cycle in which pregnancy occurs. Ovulation rate was determined by counting corpora lutea of pregnancy.

Fetal rate

The average number of fetuses per pregnant doe.

Ova loss rate

The difference between the number of fetuses present in a given number of pregnant does and the number of corpora present, expressed as a percentage of the number of corpora. Early embryonic deaths and complete resorption of fetuses could not be detected and if such phenomena occurred they were considered as ova losses. The occurrence of polyovular follicles could have resulted in undetected ova losses but Gibson (1957) reported that such follicles rarely occur in white-tailed deer.

Prenatal mortality

Fetal deaths suffered between implantation and parturition.

Pregnancy rate

Percentage of any age class pregnant during a given gestation period.

Reproductive potential

The maximum ability of a species, and hence a population, to produce offspring (Krumholz et al. 1957).

Environmental resistance

The combined effects of all the factors of the environment that tend to reduce the numbers of animals present and thereby inhibit the full realization of the reproductive potential (Krumholz et al. 1957).

Fertility

The following quotation from Cheatum and Severinghaus (1950) adequately explains the use of the term.

The term "fertility" is used here to denote the state of productiveness. It encompasses both qualitative and quantitative aspects of reproduction. The ability to reproduce as evidenced by ovulation is a qualitative character, whereas the number of ova produced and embryos developing therefrom is a quantitative character, more accurately defined by "fecundity". However, since fertility is a basic quality and antecedent to productivity, and since measurement of its variations may be made by quantitative study (e.g., number of ova and embryos produced), it is broadly used to include the total picture of productiveness.

LITERATURE REVIEW

During the past 18 years much information has been recorded in the wildlife literature which illustrates that fertility of deer varies with geographic location. The following are among the contributing authors: Morton and Cheatum (1946), Cheatum and Severinghaus (1950), Illige (1951), Shaw and McLaughlin (1951), Robinette et al. (1955), Dahlberg and Guettinger (1956), Gill (1956), Robb (1959), Jenkins and Bartlett (1959), Adams (1960), Noble (1960) and Julander, Robinette and Jones (1961).

Morton and Cheatum (1946) found that white-tailed deer from the central Adirondacks of northern New York had a significantly lower fetal rate and pregnancy rate than deer from southern New York. The lower fertility of the northern deer was attributed to a persistent low plane of winter nutrition and to a possible deficiency of one or more essential elements. In a more detailed discussion of regional variation in fertility of white-tailed deer in New York, Cheatum and Severinghaus (1950) attributed lowered fertility in the Adirondacks largely to severe winters and continued overpopulation due to inadequate harvests. Brohn and Robb (1955) and Robb (1959) found that white-tailed deer in Missouri showed regional variations in weight and fertility that apparently were due to variations in soil fertility and the fact that some herds had exceeded carrying capacity. Jenkins and Bartlett (1959) attributed lowered productivity of some deer herds in Michigan to food shortages. Julander et al. (1961) studied two herds of mule deer (Odocoileus hemionus hemionus) in Idaho and Utah from areas of good and poor quality summer range. Fertility and weight were severely reduced in the herd summering on overgrazed

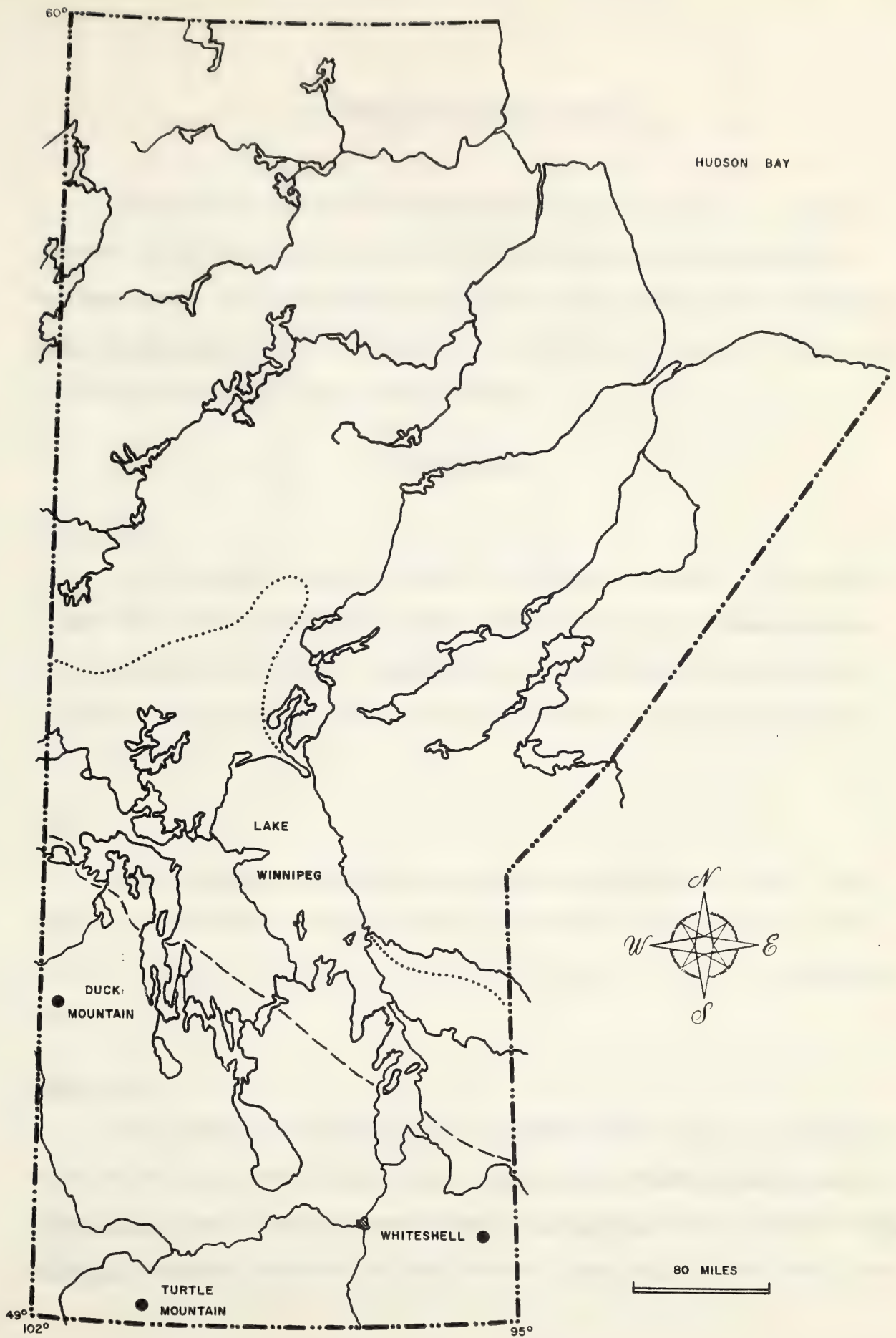
range. Although Gill (1956) found regional variation in size and fertility among white-tailed deer in West Virginia he was unable to discover any soil, food or climatic factors to explain the variation.

Ovulation rates and fetal rates have been widely used in calculations of anticipated fawn crop. Such calculations generally ignore, with some justification, the possibility of postnatal fawn losses. Severinghaus (1951), using an 86-acre enclosure in New York State, found that during the first 2 years of study when food was abundant the enclosed white-tailed deer had an average rate of increase of 1.9 fawns per doe. During the following 2 years when there was a shortage of food the rate of increase was only 0.43 fawns per doe. This low rate of increase was attributed to severely lowered fetal and pregnancy rates resulting from inadequate nutrition rather than to losses of newborn fawns. However, recent work done at Cusino, Michigan, indicates that post-partum fawn losses can exceed 90 percent of fetal counts because of inadequate winter and spring diets of the does (Verme 1962).

Considerable attention has been paid to breeding among white-tailed deer fawns since it was first reported by Cheatum and Morton (1942). Morton and Cheatum (1946) found that 36.3 percent of fawns were pregnant in southern New York State while only 4.2 percent were pregnant in the Adirondacks. The fawn class markedly indicated the difference in fertility of the two herds. Since then Cheatum and Severinghaus (1950) and Robb (1959) have shown that fertility of female fawns is a good indicator of range quality. Julander et al. (1961) found that among mule deer, where fawn breeding is almost nonexistent, fertility of the yearling does best reflected range quality.

To the best of my knowledge no previous studies of reproduction have been carried out on white-tailed deer near the northern extremity of their range.

Fig. 1. Outline map of Manitoba showing approximate centers of study areas, northern limit of white-tailed deer (dotted line) and northern limit of huntable populations (broken line).



DESCRIPTION OF STUDY AREAS

Locations of the three study areas are shown in Fig. 1. They are referred to in this thesis as the Whiteshell, Turtle Mountain, and Duck Mountain areas. The following descriptions, taken largely from the Economic Atlas of Manitoba (Manitoba Department of Industry and Commerce 1960), serve to illustrate their distinct characteristics.

Whiteshell

Physiography

The Whiteshell area lies within the Canadian Shield. It is characterized by rolling, ice-scoured upland and rock outcrop. Surface deposits are predominantly granitic. Approximately 40 to 60 percent of the area is covered by bogs and lakes. The elevation is between 1,000 and 1,100 feet above sea level.

Soils

Grey Wooded, Podzol soils cover the entire Whiteshell area. These soils are formed from acid parent materials derived from crystalline rocks. They are strongly leached, lack lime carbonate and are inferior agricultural soils.

Vegetation

Both Northern Coniferous Forest and Mixed Woods types of vegetation occur in the area. Well drained sites support good stands of white spruce (Picea glauca) and trembling aspen (Populus tremuloides) with jack-pine (Pinus banksiana) commonly occurring on sand ridges. Less well drained sites have

black spruce (Picea mariana) with some black ash (Fraxinus nigra) and northern white cedar (Thuja occidentalis). Poorly drained areas support tamarack (Larix laricina) and an understory of Labrador tea (Ledum groenlandicum). Hazel (Corylus cornuta), alder (Alnus spp.), blueberry (Vaccinium myrtilloides), and dogwood (Cornus spp.) are numerous on better drained sites.

Climate

The average annual precipitation is 22 inches and snowfall is 50 to 55 inches. Mean January temperature is about 0 F.

Turtle Mountain

Physiography

Turtle Mountain is a flat-topped range of morainic hills rising to a height of 2,500 feet as compared to the 1,600 to 1,700 foot elevation of the surrounding plains. Numerous small lakes and meadows are situated on the plateau. Turtle Mountain covers an area approximately 20 miles across and 30 miles long astride the International Boundary between Manitoba and North Dakota. Surface deposits are clay, sand, and sandstone.

Soils

Well drained Grey Wooded soils, developed on mixed boulder till, cover most of the area. A lime carbonate accumulation above the boulder till substratum tends to make the soils slightly alkaline but they are considered to be fertile agricultural soils. Surrounding Turtle Mountain up to approximately the 1,800 foot contour level, is a belt of very fertile Shallow Black soils that were developed on calcareous till.

Vegetation

The natural vegetation of Turtle Mountain varies from Broadleaf Forest to Wooded Grassland. Trembling aspen is the dominant tree species on the plateau while bur oak (Quercus macrocarpa) is the characteristic tree of the slopes. White birch (Betula papyrifera) and green ash (Fraxinus pennsylvanica) are common. Elm (Ulmus americana) and maple (Acer negundo) have scattered distribution but no coniferous trees occur naturally in the area.

Shrub vegetation consists of saskatoon (Amelanchier alnifolia), choke-cherry (Prunus virginianus), buckbrush (Symphoricarpos spp.), hazel, red-osier dogwood (Cornus stolonifera) and viburnums.

Wheat, oats, barley and alfalfa are agricultural crops commonly grown on the slopes of Turtle Mountain.

Climate

The average annual precipitation is 19 to 20 inches and snowfall averages 50 to 55 inches. The mean January temperature is +2 F to +3 F.

Duck Mountain

Physiography

Duck Mountain is a series of sharply undulating terminal and ground moraines cut by several abrupt river valleys and dotted with numerous deep lakes and swamps. Surface deposits are sand, sandstone, and shale. The highest elevation is 2,727 feet but my study area was located between the 2,000 and 2,200 foot levels.

Soils

Grey Wooded soils cover most of Duck Mountain and are able to support excellent vegetative growth. Upland sites are well drained but lowlands only poorly so.

Vegetation

Duck Mountain vegetation is chiefly of the Mixed Woods type. Trembling aspen, white birch, white spruce and jack-pine are the major upland trees while black spruce and tamarack occupy the less well drained sites. Hazel is the dominant shrub but saskatoon, chokecherry, red-osier dogwood, alder and viburnums are abundant. There are extensive tracts of willow (Salix spp.) in poorly drained areas.

Climate

Precipitation annually amounts to 16 to 17 inches. Snowfall averages about 45 inches and the mean January temperature is -3 F to -4 F.

Comparison of Habitat Quality

Habitat quality, on the basis of soil fertility, vegetation types and the availability of agricultural crops, is best in Turtle Mountain, poorest in the Whiteshell and intermediate in Duck Mountain.

MATERIALS

For this study 159 female white-tailed deer were collected. The age distribution of the sample and the year and place of collection are shown in Table 1.

Hall and Kelson (1959) list Dama (= Odocoileus) virginianus dacotensis as the only subspecies of white-tailed deer occurring in Manitoba. This was done in error and Hall (1963 pers. commun.) believes that O. v. borealis extends into Manitoba from the southeast and a line approximating their western extremity would fall somewhere west of the Whiteshell area. Kellogg (1956) shows the two subspecies meeting at the Red River in Manitoba. Hall states (in litt.):

I would expect the two mentioned subspecies to intergrade in a broad belt. If such is the case, comparable (as to age, sex and season) specimens from places 15 miles or even 20 miles apart in Manitoba might be indistinguishable; perhaps comparable specimens from places 50 to 60 miles apart (on an east-west line) would, on the average, be slightly different.

It is therefore fairly certain that O. v. dacotensis occur in Turtle Mountain which is at least 100 miles to the west of the supposed boundary of the two subspecies. The Whiteshell collections were made a minimum of 80 miles to the east of this boundary and therefore are probably O. v. borealis. Deer from Duck Mountain are almost certainly O. v. dacotensis.

It is not known what differences may exist between subspecies when

considering reproductive characteristics, but the existence of differences is a possibility that cannot be disregarded.

Table 1. Place of origin and age composition of female white-tailed deer collected during the winters of 1961, 1962 and 1963.

	WHITESHELL			TURTLE MOUNTAIN			DUCK MOUNTAIN		
	Fawns	Year-lings	Adults	Fawns	Year-lings	Adults	Fawns	Year-lings	Adults
1961	3	5	13	2	1	16	4	1	3
1962	3	4	12	7	3	11	5	2	9
1963	4	1	11	7	3	12	1	4	12
Total	10	10	36	16	7	39	10	7	24

METHODS

This study was designed and initiated in the summer of 1960 as a 2-year project. At the end of that time it was realized that a third year of collections was necessary to obtain adequate samples. Field collections were extended 1 year and the project terminated in April 1963.

Field Collections

Conservation Officers of the Manitoba Department of Mines and Natural Resources carried out the field collections under my supervision. One Conservation Officer was responsible for each area yearly.

Adult deer were collected from late December to mid-April each year. Fawns were usually not collected until February. The purpose of this delay was to allow late maturing fawns to breed before collections were made.

In the Whiteshell and Turtle Mountain, deer were usually collected along roads and trails, although some were taken in more inaccessible places by hunting on foot or from a power toboggan. Prior to making some collections, it was possible to view a deer, or group of deer, through binoculars. The accidental shooting of males was reduced in this manner.

Deer in the Duck Mountain area were the most difficult to get. Access was limited for wheeled vehicles, necessitating the use of tracked snow vehicles and occasionally snowshoes. Field autopsies in all areas were often hindered by low temperatures. This problem was particularly acute in the Duck Mountain area.

Field autopsies included taking standard measurements of height, girth, length, hindfoot, tail, total weight and field-dressed weight. The lower jaw and reproductive tract were collected from all animals. The right femur and kidneys with surrounding fat were collected for use in determining physical condition during the final year of study.

The person doing the field autopsy often encountered difficulty in avoiding frostbite while working with bare hands. It was later discovered that by wearing either surgical rubber gloves or disposable plastic gloves it was possible to keep one's hands dry and the body heat of the deer would keep them warm. There were of course problems of having wet gloves freeze to the knife blade, bone saw, scale, or any metal object that had to be handled. Nevertheless, gloves were very useful in doing autopsies in cold weather.

Handling of Materials

Materials collected in the field for examination in the laboratory were placed in polyethylene bags, tagged and frozen. In the laboratory the reproductive tracts were thawed and the ovaries were put in 10 percent formalin. A few fetuses were preserved in 10 percent formalin but most were examined in a fresh state.

Fawn reproductive tracts were inflated with 10 percent formalin in a manner similar to that described by Haugen (1963). These tracts were examined only if the ovaries contained a corpus luteum.

Age Determination

Fetuses

Two methods of determining fetal age were considered. A fetal growth

curve is employed in one method (Cheatum and Morton 1946) while the other uses the appearance of morphological features and physical size to assign age (Armstrong 1950).

To age a fetus by the growth curve method it is necessary to obtain the forehead to rump measurement (in mm) which is entered on the y-axis of the growth curve and the age is read on the x-axis. This method is objective and easily used. It is based upon the fact that fetuses tend to increase in length according to a definite mathematical formula during the gestation period. There are however, a number of factors that cause the growth rate of individual fetuses to deviate from the general formula. For instance, Verme (1963) found that fetal growth was retarded if the dam was in poor physical condition. This effect became noticeable at 133 days' gestation and was most severe during the last one-third of gestation. Severinghaus and Cheatum (1956) reported that the weight of a fawn at birth is related to the weight of the dam and that the weight of male fawns was proportionately greater than that of females which suggests that the size of a fetus at any given stage of gestation is affected by the size of the dam and the sex of the fetus. Some variation in size may also be found among single, twin and triplet fetuses of the same age.

The morphological key devised by Armstrong (1950) has one major theoretical advantage. External fetal features supposedly develop independently of the size or physical condition of the dam and independently of the sex of the fetus. Her key should therefore overcome the disadvantages of the growth curve method of aging. But, in fact, it does not overcome these difficulties because the 76 fetuses that her work is based upon were not specimens of known

age. Their ages were assigned with the use of the growth curve published by Cheatum and Morton (1946) which renders her key subject to the same errors that apply to aging any group of fetuses by the growth curve. Consequently I did not use the morphological key in this study but found it necessary to age fetuses by the growth curve method.

Fetal measurements were converted to age using an enlargement of the growth curve published by Cheatum and Morton (1946). In cases of twins or triplets the individual lengths were grouped and the average length was used in the age determination.

The error introduced by the disadvantages of the growth curve is probably held to a minimum because the majority of fetuses were less than 133 days of age and most does were in good condition according to criteria used by Verme (1963).

Measurements of fetuses were taken in the laboratory with calipers. Each fetus was placed on its side with its back against a board so that uniform measurements could be obtained. In order to appraise the ability of different observers to measure accurately and consistently, measurements of the same fetus were made by two observers and each repeated the measurement. Negligible differences were found for such a series.

During the first year of the study a number of fetuses were preserved in 10 percent formalin before being measured. Therefore 21 fetuses were measured in a fresh state and again after preservation in formalin. The average shrinkage was 3.25 percent and measurements of preserved fetuses were corrected accordingly. Fetuses from the final 2 years of the study were all

measured in a fresh state.

Breeding dates were calculated by subtracting the calculated age of a fetus from the date of its death. Fawning dates were estimated by adding 202 days (gestation period used by Noble 1960) to the calculated breeding date.

Fawns, yearlings and adults

All deer collected were classified as fawns, yearlings or adults on the basis of tooth eruption and wear. Fawns were recognized by the presence of M_1 and a partially erupted M_2 and yearlings by their partially erupted M_3 and the presence of deciduous or newly replaced premolars. All deer showing wear on the premolars and having fully erupted molars were classed as adults. The incisor teeth were normally not used in the classification because in many cases only the cheek teeth had been collected. Diagnostic features of age were taken from Severinghaus (1949).

The three age groups described were used in most comparisons of reproductive traits. I believed that any major reproductive differences due to age would be recognized in this manner. In addition to three age groups, the adult deer were placed into yearly age classes by counting growth layers in the cementum of the first lower molar (M_1). This method of age determination has been used by Mitchell (1963) to determine the age of red deer (Cervus elaphus) and by Flook (1963 pers. commun.) for elk (Cervus canadensis). A similar method, based upon the incisor teeth, has been used by Sergeant and Pimlott (1959) to age moose (Alces alces), by McEwan (1963) to age barren ground caribou (Rangifera tarandus groenlandicus) and by Low and Cowan (1963) to age black-tailed deer (Odocoileus hemionus columbianus).

Counts of the layers in the pad of cementum underlying M_1 in 16 jaws from deer of known age indicated that the method is satisfactory for aging white-tailed deer.

Ovary Examinations

Ovaries from the first 2 years of collections were embedded in a cornmeal-gelatin mixture essentially as described by Pimlott and Mossman (1959). While it was not my intention to make histological sections, I felt that it was desirable to make sections suitable for examination under a dissecting microscope to be certain of corpora lutea counts. Following slicing and examination, the ovaries were tied in pieces of nylon hose or cheesecloth, tagged and stored in 10 percent formalin. All ovaries were examined at least twice. Two years of examinations in this fashion were adequate to become familiar with the method of recognizing and counting corpora; therefore, the ovaries from the final year of collections were simply hardened in 10 percent formalin and slit once or twice with a scalpel. When necessary an ovary was opened like a book and placed between two glass slides for observation under low magnification. This method was found to be entirely satisfactory for interpreting ovaries from the gestation period collections.

Determination of Physical Condition

Riney (1955) found that weight of kidney fat expressed as a percentage of kidney weight is a valid index of physical condition for red deer. Therefore a kidney fat index was calculated for each deer collected during the final year of this study. Both kidneys were used to reduce variation. In addition, the central 2 inches of marrow was removed in the laboratory from the right

femurs of 34 deer of all ages with kidney fat indices ranging from low to high. Fat content of these samples was determined by a commercial chemist by petroleic ether extraction.

Statistical Treatment of Data

Calculated breeding dates were grouped into weekly intervals and ranked with the earliest week in which breeding occurred being designated as 1 and all succeeding weekly intervals numbered in consecutive order. The mean ranking of breeding dates was then calculated for each area and differences were tested for significance using "Student's" distribution of t . The distribution of t was also used to test for differences among ovulation and fetal rates while fetal sex ratios were tested using the chi-square distribution.

Since repetition of this study in the near future is out of the question it is very important that no real differences be rejected as insignificant. Therefore I have treated probability values of .10 or less as significant. Because all researchers will not agree with this approach the probability values are given for all differences considered to be significant. The reader is thus able to make his own judgement. In addition, tables presenting original data on ovulation and fetal rates include the mean values, standard errors and sample size from which P values can be quickly calculated if desired.

I offer the following quotation from Quantitative Zoology by Simpson, Roe and Lewontin (1960) as justification for this rather unusual procedure. Their statement makes very clear the need for more than blind acceptance of .05 as the level of rejection.

It not infrequently happens that an author, using the 5 per cent probability value as a criterion for rejection of a hypothesis, will reject one hypothesis under which the observations had a probability value of 4 per cent while accepting another, the observations for which had a probability of 6 per cent, without disclosing these probability values. Having chosen the 5 per cent level for rejection, this procedure is perfectly correct logically, but abhorrent biologically. On such slender threads hang many theories!

RESULTS

Breeding Season

The chronology of breeding activity of female deer from the three study areas is presented in Table 2. It is evident from this table that the annual cycle of reproductive activity commenced earlier, reached a peak and terminated earlier in the Whiteshell area than in either the Duck or Turtle Mountains. The difference in timing for adult and yearling deer between the Whiteshell and Turtle Mountain is significant ($P = .01$) as is the difference between those from the Whiteshell and Duck Mountain ($P = .01$). The difference between Turtle and Duck Mountain deer is not significant. There did not appear to be any differences among years for the same area.

The majority of does apparently were bred during the period of November 8 to 28.

Fawning Season

Table 2 also shows the estimated fawning dates for deer from the three study areas. Since these estimates are subject to all the possible errors inherent in the breeding dates as well as the probability of variation in gestation periods between deer, they probably are not as accurate as the calculated breeding dates.

It is estimated that the majority of fawns were born during the period of 29 May to 18 June.

Table 2. Calculated breeding and fawning dates of female white-tailed deer from three areas of Manitoba.

Breeding Dates	ADULTS AND YEARLINGS				FAWNS		
	Whiteshell	Turtle Mountain	Duck Mountain		Turtle Mountain	Duck Mountain	Fawning Dates
	Number	%	Number	%	Number	Number	
Oct. 11 - 17	1	2.3					May 1 - 7
Oct. 18 - 24							May 8 - 14
Oct. 25 - 31	5	11.6					May 15 - 21
Nov. 1 - 7	5	11.6	1	2.3	2		May 22 - 28
Nov. 8 - 14	11	25.6	7	16.0	3	1	May 29 - June 4
Nov. 15 - 21	10	23.3	14	31.8	11		June 5 - 11
Nov. 22 - 28	8	18.6	12	27.3	8	1	June 12 - 18
Nov. 29 - Dec. 5	3	7.0	3	6.8	6		June 19 - 25
Dec. 6 - 12			2	4.5		1	June 26 - July 2
Dec. 13 - 19			3	6.8			July 3 - 9
Dec. 20 - 26			2	4.5	1		July 10 - 16
Jan. 3 - 9						1	July 24 - 30
Jan. 17 - 23						1	Aug. 8 - 14

Ovulation Rates

Table 3 shows ovulation rates for three age groups according to area and for seven age groups from all areas. Turtle Mountain adults had an ovulation rate that is significantly higher ($P = .02$) than that of Whiteshell adult does. The differences between rates for Duck Mountain adult does and adult does from the other two areas are not significant. The ovulation rate for Turtle Mountain yearlings is significantly higher ($P = .07$) than that of Duck Mountain yearlings and is also significantly higher ($P = .01$) than that of Whiteshell yearlings. Whiteshell and Duck Mountain yearling rates are not significantly different. Fawn ovulation rates are not significantly different between the Duck and Turtle Mountain groups but note the absence of ovulation among Whiteshell fawns.

No significant differences are present between any of the age groups of animals older than yearlings. Both yearlings and fawns differ significantly from adults ($P = \text{less than } .05$) but the difference between fawns and yearlings is not significant. It must be realized that these rates were calculated for grouped variates and the numbers contributed by each area are not necessarily equal.

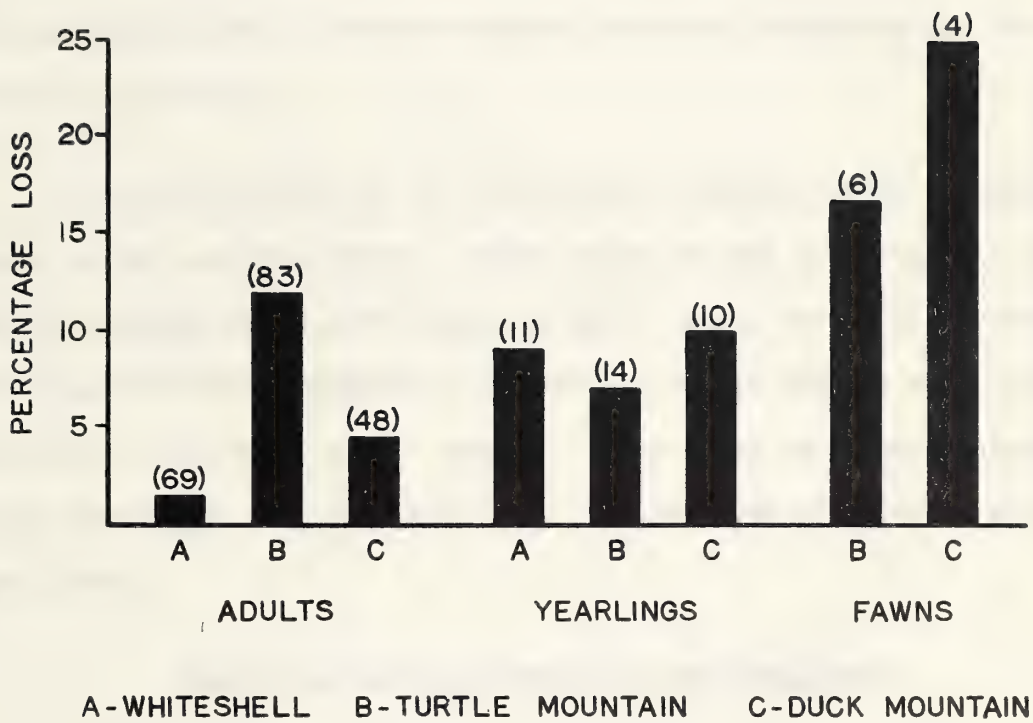
Ova Losses

Ova loss rates presented in Fig. 2 show that Turtle Mountain adults suffered high rates of loss compared with Whiteshell and Duck Mountain adults. There appears to be a tendency for loss rates to be higher among yearlings and fawns but definite statements cannot be made on the basis of such small samples.

Table 3. Ovulation rates by age group and area for white-tailed deer in Manitoba.

Age Group (years)	Whiteshell	Turtle Mountain	Duck Mountain	All Areas
$\frac{1}{2}$		$1.50 \pm .29(4)$	$1.33 \pm .33(3)$	$1.43 \pm .20(7)$
$1\frac{1}{2}$	$1.22 \pm .15(9)$	$2.00 \pm .22(7)$	$1.43 \pm .20(7)$	$1.52 \pm .12(23)$
$2\frac{1}{2}$)				$1.93 \pm .07(15)$
))				
$3\frac{1}{2}$)				$2.00 \pm .00(16)$
))				
$4\frac{1}{2} - 7\frac{1}{2}$)	$1.92 \pm .06(36)$	$2.18 \pm .08(38)$	$2.00 \pm .09(24)$	$2.09 \pm .10(33)$
))				
$8\frac{1}{2} - 9\frac{1}{2}$)				$2.17 \pm .12(18)$
))				
$10\frac{1}{2}$ plus)				$2.00 \pm .11(13)$

Fig. 2. Ova loss rates for three age groups of white-tailed deer from three areas of Manitoba (numbers of ova shed are shown in parentheses).



Fetal Rates

Table 4 presents fetal rates that can be compared with ovulation rates given in Table 3. Adult fetal rates are remarkably similar among areas and differences are not significant. The difference in rates between Turtle Mountain and Whiteshell yearlings is significant ($P = .01$) as is the difference between Turtle Mountain and Duck Mountain yearling rates ($P = .08$). The difference between Duck Mountain and Whiteshell yearling rates is not significant. The higher fetal rate of Turtle Mountain fawns was caused by the occurrence of one set of twins.

Fetal rates given in the last column of Table 4 show the same general pattern as the ovulation rates. Adult rates are all significantly higher than fawn and yearling rates ($P =$ less than $.05$). Among the adults, rates of $8\frac{1}{2}$ - and $9\frac{1}{2}$ -year-old does compared to $2\frac{1}{2}$ -year-old and to $10\frac{1}{2}$ and older does show a P value of $.10$ in both cases. However, since these rates were calculated using unequal numbers of deer from each area, the observed differences are of dubious significance.

Yearly Variation in Ovulation and Fetal Rates

The data presented in Table 5 were calculated by grouping the individual adult variates from all areas for each of the 3 years of the study. A comparison of ovulation rates for 1961 and 1962 shows a significant difference ($P = .01$) as does a comparison between 1962 and 1963 means ($P = .03$). There is not a significant difference between 1961 and 1963 means. A similar comparison of fetal rates shows the 1961 mean to be significantly higher ($P = .03$) than the 1962 mean while neither the 1962 to 1963 or the 1961 to 1963 comparisons show significant differences. Nevertheless, the 1962 mean is lower by inspection than the 1963 mean.

Table 4. Fetal rates by age group and area for white-tailed deer in Manitoba.

Age Group (years)	Whiteshell	Turtle Mountain	Duck Mountain	All Areas
$\frac{1}{2}$		$1.25 \pm .25(4)$	$1.00 \pm .00(3)$	$1.14 \pm .14(7)$
$1\frac{1}{2}$	$1.11 \pm .11(9)$	$1.71 \pm .25(7)$	$1.29 \pm .18(7)$	$1.39 \pm .10(23)$
$2\frac{1}{2}$)				$1.80 \pm .11(15)$
))				
$3\frac{1}{2}$)				$1.88 \pm .09(16)$
))				
$4\frac{1}{2} - 7\frac{1}{2}$)	$1.89 \pm .07(36)$	$1.92 \pm .09(38)$	$1.92 \pm .10(24)$	$1.98 \pm .10(33)$
))				
$8\frac{1}{2} - 9\frac{1}{2}$)				$2.05 \pm .10(18)$
))				
$10\frac{1}{2}$ plus)				$1.77 \pm .12(13)$

Table 5. Mean yearly ovulation and fetal rates of adult white-tailed deer from three areas of Manitoba.

	1961	1962	1963
Ovulation rates	$2.19 \pm .07(31)$	$1.84 \pm .09(32)$	$2.09 \pm .06(35)$
Fetal rates	$2.03 \pm .09(31)$	$1.78 \pm .07(32)$	$1.91 \pm .08(35)$

Pregnancy Rates

All yearling and adult does were pregnant (Fig. 3) with the exceptions of one adult from Turtle Mountain and one yearling from the Whiteshell. Breeding among Whiteshell fawns was not detected but because of the small sample size it cannot be stated that no Whiteshell fawns bred during the period of study.

Prenatal Mortality

Two cases of fetal resorption were discovered during this study. Both were found in does from Turtle Mountain. Resorption had commenced before day 80 in both cases but the exact dates are unknown. One doe was also carrying two healthy fetuses while the other carried one. One dead fetus was determined to have been a male but sex determination was not possible for the other dead fetus. Both does had good fat reserves.

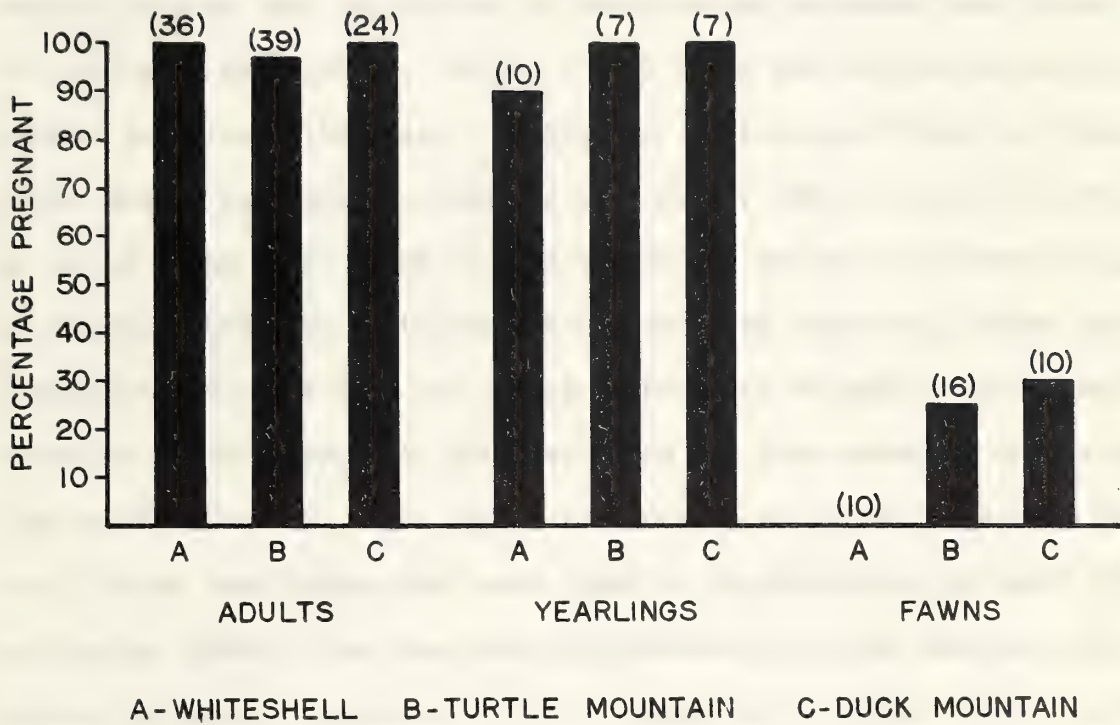
Size

Comparisons of size were based upon overall length minus tail length. Variability of size within age groups from any of the areas was considerable and because of this comparisons between areas for fawns and yearlings could not be made. Does 3 years of age and older were smallest ($P = .01$) in the Duck Mountain area as shown by the following measurements (in cm): Whiteshell - $150.6 \pm 1.26(28)$; Turtle Mountain - $149.6 \pm 0.95(34)$; Duck Mountain - $144.4 \pm 1.71(20)$.

Physical Condition

Fig. 4 is a scatter diagram showing kidney fat indices of yearling

Fig. 3. Pregnancy rates of white-tailed deer from three areas of Manitoba (sample size shown in parentheses).



and adult deer collected in 1963, plotted against weekly intervals of time. Although there is considerable variation in condition of deer from each area relative to time, there do not appear to be any differences in rate of condition loss between areas.

The amount of fat in the femur marrow was determined for 34 deer and is plotted against the kidney fat index in Fig. 5. It is evident from this scatter diagram that fat content of femur marrow decreased when kidney fat fell below an index of 30. Harris (1945) found that extreme malnutrition was evident in white-tailed deer 2 weeks after depletion of femur fat began and deaths due to malnutrition occurred soon after. Since kidney fat indices were as low as 30 by early March in both the Turtle and Duck Mountains (Fig. 4) it is probable that some deaths due to malnutrition occurred in those areas. Unfortunately only one deer was collected from the Whiteshell during March and therefore direct comparison with deer from the other areas is not possible for that month. However, femur marrow fat content was below 25 percent for two out of three deer tested that were taken in the Whiteshell in April (Fig. 4). As Cheatum (1949b) found deer dead from malnutrition and exposure with femur marrow fat content levels of 20 to 25 percent it is evident that some Whiteshell deer probably died of malnutrition in the spring of 1963.

Sex Ratios of Fetuses

Table 6 shows sex ratios for 174 fetuses. Chi-square tests showed no significant differences from a 100 to 100 ratio.

Reproductive Anomalies

Three adult does with small velvet-covered button antlers were

collected during the study. All were carrying fetuses and there did not appear to be any other anatomical peculiarities.

Fig. 4. Scatter diagram of kidney fat indices of yearling and adult white-tailed deer from three areas of Manitoba, plotted against time.

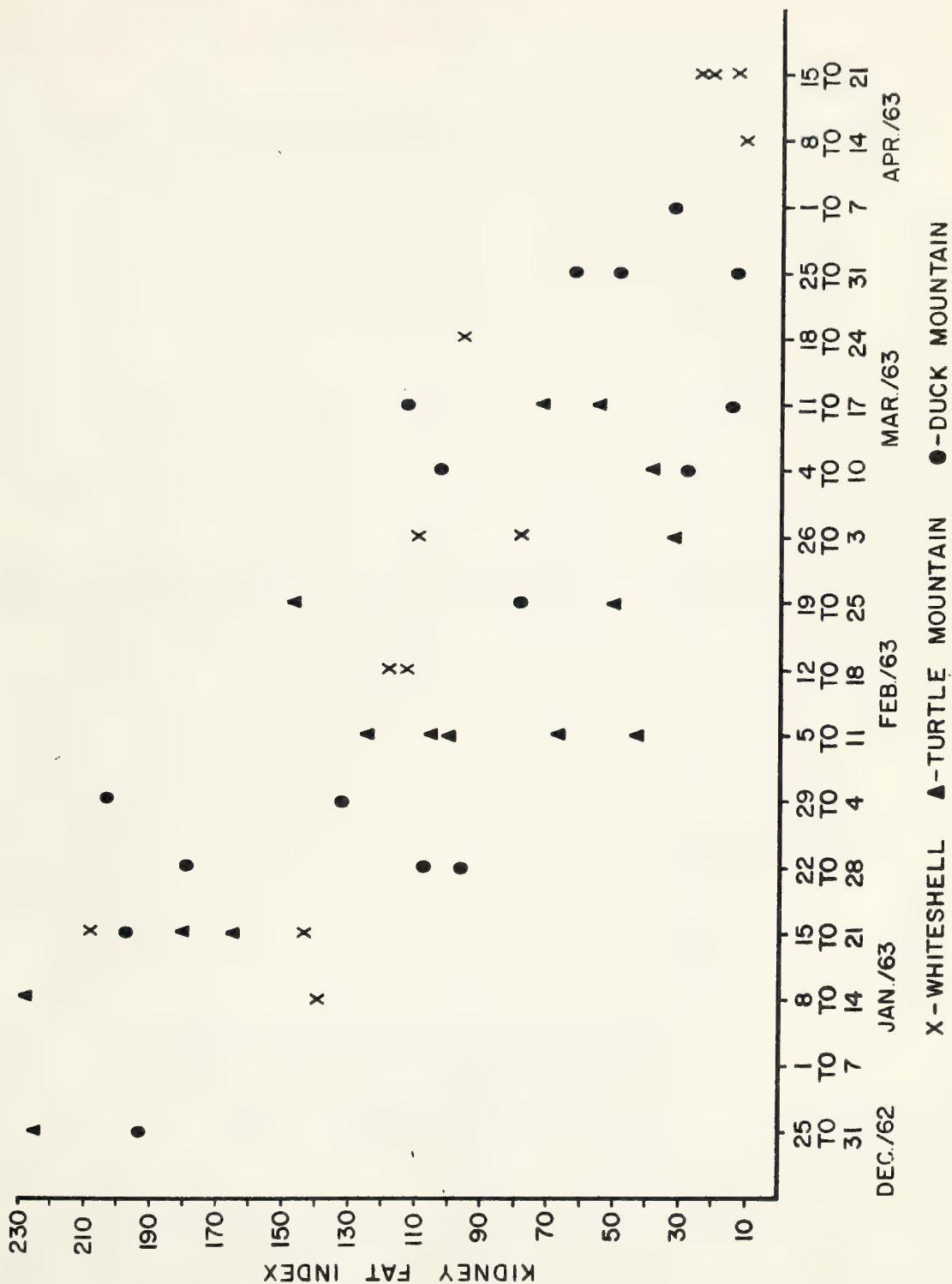


Fig. 5. Scatter diagram of kidney fat indices plotted against percentage femur marrow fat of 34 deer from Manitoba.

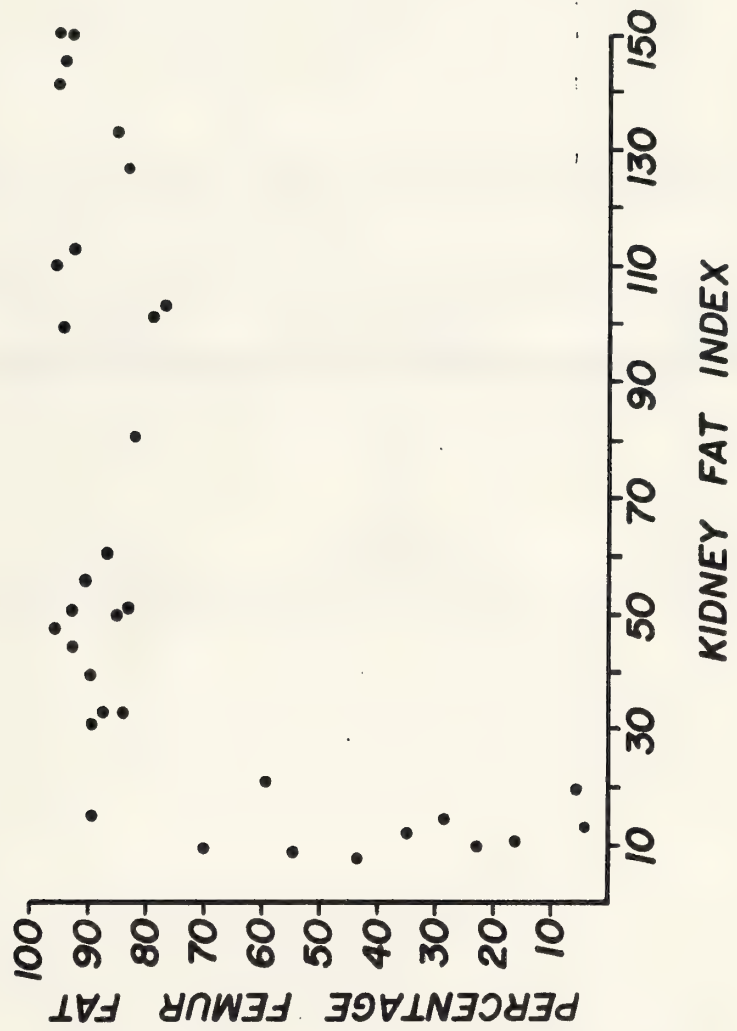


Table 6. Sex ratios of white-tailed deer fetuses from three areas of Manitoba.

	Whiteshell	Turtle Mountain	Duck Mountain	Total
Male	25	31	31	87
Female	31	37	19	87
Ratio	81:100	84:100	163:100	100:100

DISCUSSION

Breeding Chronology

The relative timing of the breeding seasons was unexpected. Since Duck Mountain lies approximately 180 and 130 miles further north than Turtle Mountain and the Whiteshell area respectively (Fig. 1) it was expected that deer would breed earlier in the Duck Mountain area while deer from the other study areas were expected to breed at approximately the same time. The following discussion points out reasons justifying these expectations and covers possible causes of the observed breeding chronology.

The literature reveals a general pattern of earlier breeding as latitude increases. For example, Sonora white-tailed deer (O. v. couesi) of northwestern Mexico breed about mid-January (McCabe and Leopold 1951); a majority of white-tailed deer (O. v. texanus) from southern Texas are bred between 15 December and 3 January (Illige 1951); a majority of white-tailed deer in Massachusetts breed between November 15 and 23 (Shaw and McLaughlin 1951); while in Michigan and Maine most deer are bred about the middle of November (Jenkins and Bartlett 1959, Banasiak 1961). This south to north trend has also been observed within New York, Alabama and Mississippi (Cheatum and Morton 1946, Adams 1960, Noble 1963 pers. commun.). A notable exception to this pattern was reported by Bischoff (1957) who found that among five herds of black-tailed deer in California there is a tendency for northern herds to breed later although seven herds of mule deer show the usual earlier breeding among northern herds. Loveless (1959) reports that the south to north breeding pattern does not hold for all populations of white-tailed deer in Florida.

Although most reports have dealt with breeding chronology it must be realized that it is the timing of the fawning seasons that is important and breeding seasons are only an evolutionary adaptation to ensure that young are born at a time when their chances of survival are maximal. Clegg and Ganong (1959) point out that reproductive photoperiodism, the dependence of breeding activity on changes in incident illumination, is probably a result of natural selection in temperate zones as it causes young to be born during the spring of the year. McCabe and Leopold (1951) found that Sonora white-tailed deer dropped their fawns during the peak of vegetative growth which was supposedly the most opportune time for fawn survival. Their discussion indicates that breeding seasons of white-tailed deer in northern mesophytic areas are also timed to result in fawns being born at the peak of vegetative growth. This point will be returned to later but first it is necessary to discuss some of the factors that control breeding.

Latitudinal climatic factors

The general pattern of earlier breeding as latitude increases is attributed chiefly to environmental factors as suggested by Cheatum and Morton (1946) who speculated that deer bred earlier in northern than in southern New York because of the effects of "latitude, altitude, light intensity and other external influences". Later, Severinghaus and Cheatum (1956) similarly concluded that there appear to be latitudinal climatic factors governing the onset, peak and duration of the mating season of white-tailed deer. This is presumably a reference to temperature as well as light. Certainly temperature has been considered important by other authors. For example, Darling (1937) considered that breeding activity of red deer in Scotland was affected by temperature and Noble (1963 pers. commun.) suspected that lower temperature

in northern Mississippi was a factor tending to make deer breed earlier there than in the southern part of the State. Since autumn frosts occur in the Duck Mountain area earlier than in the Whiteshell or Turtle Mountain and since Duck Mountain is the most northerly study area, it appears that latitudinal climatic factors are only of secondary importance in the control of deer breeding within Manitoba.

Genetic factors

Adams (1960) found that over a period of years white-tailed deer from northern Alabama, confined at Auburn in southern Alabama, had a mean breeding date of 31 December. Deer of southern stock, penned under the same conditions, had a mean date of 29 January. Genetic factors apparently caused the two groups of deer to react differently to the same set of environmental influences. Since two subspecies are probably involved in Manitoba it is possible that the genetic make-up of the three populations is sufficiently different to account for the observed breeding chronology. This possibility could only be checked by confining deer from the different areas under the same conditions to observe their reproductive behaviour.

Nutritional factors

Verme (1962) indicated that does losing their fawns at or shortly after birth are able to regain top physical condition sooner than lactating does and will therefore breed earlier. Since Verme also found that the degree of deterioration of physical condition over winter has a profound effect upon survival of newborn fawns he postulated that does on poor range would breed earlier than does on good range. This presumably occurs because an early-bred doe is subject to greater energy requirements during the winter than one that is bred late and therefore her physical condition will deteriorate to a greater

extent by the end of winter. The early-bred doe not only is in poorer condition but has less time in which to recuperate before giving birth, thus decreasing her fawn's chances of survival. Verme (1962) suggested that this could be "an insidious, self-perpetuating population phenomenon".

The early breeding of Whiteshell deer can be explained by this mechanism if it is assumed that early postnatal fawn losses are high. Although Fig. 4 gives no indication that loss of condition was greater in the Whiteshell than in the other areas there is some circumstantial evidence to indicate a low ratio of juveniles to adults in the Whiteshell. During three winters of collecting deer it was found that adult does were readily obtained in the Whiteshell but fawns were very difficult to get. The opposite situation was encountered in Duck Mountain (for two out of three winters) and in Turtle Mountain indicating that fawns were relatively scarce in the Whiteshell. Additional data should be collected regarding juvenile to adult ratios to corroborate this.

Theoretical Effects of Photoperiod and Temperature in Northern Areas

If it is a valid assumption that breeding seasons are timed to result in fawns being born during the period of peak vegetative growth, as suggested by McCabe and Leopold (1951), then it is apparent that within northern mesophytic areas fawning should be progressively later with increasing latitude since that is the general pattern followed by spring vegetative growth. However, if deer in northern areas were stimulated to breed by the same light intensities as deer in more southerly areas, their breeding season and hence fawning season would be earlier with increasing latitude. Temperature would have a similar effect. The dis-synchrony thus created between fawning

and vegetative growth would be greater with increasing latitude and would be limiting to the northward expansion of the species. Since the observed breeding chronology within Manitoba does not follow the expected pattern and since a majority of deer in New York, Massachusetts, Maine, Michigan and Manitoba all breed within the month of November, I do not think the assumption made by McCabe and Leopold is valid in northern areas such as Manitoba. Because snow hinders deer movement it is an obvious truth that small fawns have less chance of surviving their first winter than do large fawns and therefore it seems probable that in northern areas the optimum fawning time for survival (to breeding age) is a balance between increasing immediate postnatal losses due to early births and increasing winter losses because of late births. If this is so, the fawning seasons should not coincide with the peak of vegetative growth in northern areas.

In either case, even minimum fawn losses will tend to be higher in northern areas than in southern areas, thus lowering the capacity of northern deer herds to increase.

Influence of Hunting on Breeding

Many sportsmen believe that does may not be serviced if the hunting season coincides with the breeding season, thereby resulting in barren does and loss of fawn production. During the organization of this study some concern was expressed in this regard. However, Fig. 3 shows that the deer collected had a very high pregnancy rate and out of 77 deer older than fawns that were taken in hunted areas, only 1 was not pregnant despite the fact that the hunting seasons overlapped a major portion of the breeding seasons during this study. Obviously loss of production due to breeding failure is very small.

But Table 2 shows that breeding activity in heavily hunted Turtle Mountain was prolonged more than in the other areas suggesting that some of the late bred deer may well have been missed during their first estrus because of hunting activity but were subsequently bred during their second estrus. While late breeding may have slight disadvantages in a deer population under natural control, it is desirable in hunted populations since late bred does require a lower energy intake over the winter and as a result will be in better condition to give birth to fawns and support them and hence more fawns will survive until hunting season. A second advantage to concentrating hunting activity during the peak of breeding is that the proportion of bucks to does in the kill should rise, for as Ruhl (1956) points out, bucks are less wary at this time and are more readily shot. Increased fawn survival to hunting season and an increased buck-to-doe ratio in the kill would be significant to management.

Influence of Range Quality on Ovulation and Ova Loss

The ovulation rates shown in Table 3 rank in accordance with my appraisal of habitat quality. However, adult does from Turtle Mountain suffered a surprisingly high rate of ova loss compared to those from the other areas (Fig. 2). A review of the literature shows that it is more common to find a greater percentage of ova being lost by does with low ovulation and pregnancy rates. This was observed by Morton and Cheatum (1946) for white-tailed deer and by Julander et al. (1961) for mule deer. But these authors were comparing deer from very poor range with deer from good or excellent range whereas my comparisons are between deer from fair, good and excellent range. It appears that the increased losses shown by these workers for deer on poor range resulted from reproductive impairment due to nutritional

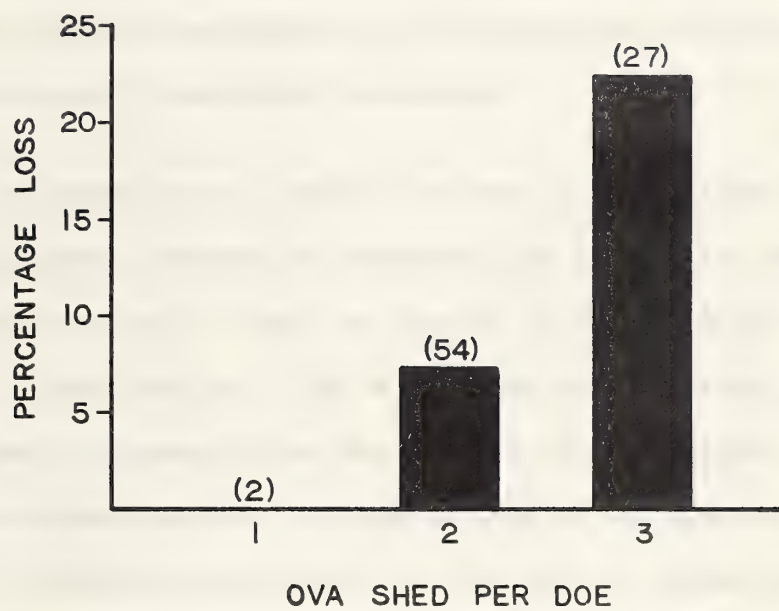
inadequacies. I believe that the high loss suffered by Turtle Mountain does was due to a very high plane of nutrition that resulted in an increased frequency of triple ovulations and thus led to higher losses.

Moustgaard (1959) stated that the lamb crop from domestic sheep can be increased by 10 to 20 percent by "flushing" which entails raising the concentrated food intake of ewes some time before breeding. The practice is most successful when ewes are previously on a less than optimal diet. Nalbandov (1958) states that this practice also works with swine but that embryonal mortality is increased.

Turtle Mountain deer are exposed each year to conditions that are analogous to flushing. During the summer they live to a great extent on naturally occurring food and during this period many does are subjected to lactational stress, but at about the beginning of September they make increasing use of agricultural crops such as alfalfa, coarse grains and flax. Lactational stress is also reduced around this time, allowing does to make full use of their increased quality food, thus resulting in a greater number of triple ovulations than would otherwise have occurred. Robinette et al. (1955) found that in mule deer the percentage of ova lost increased with the number shed, which is what happened in Turtle Mountain does (Fig. 6). The greater part of the losses suffered can be accounted for in this manner.

Table 5 shows that the adult deer collected in 1962 had a significantly lower ovulation rate compared to collections from 1961 and 1963, which strongly indicates that range quality was lower during the summer and autumn of 1961 than it was during the other 2 years of the study. This was probably due to the fact that 1961 was the driest year on record for Manitoba. The

Fig. 6. Percentage of ova lost relative to number shed per Turtle Mountain adult white-tailed doe (numbers of ova shed are shown in parentheses).



decreased percentage ova loss for 1962 (indicated by Table 5) appears to be a compensatory mechanism counteracting the effects of reduced range quality.

Influence of Age on Ovulation and Fetal Rates

Reproductive performance of yearling does is sometimes grouped with reproductive performance of adult deer (Morton and Cheatum 1946, Cheatum and Severinghaus 1950). Tables 3 and 4 show that yearlings, as well as fawns, have ovulation and fetal rates that are significantly lower than for adults thus clearly showing the importance of considering yearling reproductive performance separately from older age classes.

Ovulation rates of adult deer show no significant differences between age groups although by inspection the rates were lowest in $2\frac{1}{2}$ -year-old deer and rose until a peak was reached by $8\frac{1}{2}$ - and $9\frac{1}{2}$ -year-olds after which there was a slight decline. The fetal rates show the same pattern and the rate of $8\frac{1}{2}$ - and $9\frac{1}{2}$ -year-old deer may be significantly higher than rates of the youngest and oldest adults, although as pointed out previously, these differences are of dubious significance. In any case it appears that senility has only a negligible effect on fertility as the oldest deer show ovulation and fetal rates that are equal to those of young adult age classes. In addition, there is no indication of lowered pregnancy rates among old deer. However, since old deer suffer more during winter than young adults, it is possible that survival of newborn fawns is lower among such deer.

Yearlings Versus Fawns as Indicators of Range Condition

Morton and Cheatum (1946) and Cheatum and Severinghaus (1950) compared fertility of fawns with fertility of older deer on a regional basis

within New York and found that fawn fertility varied more between regions than did fertility of older deer. Julander et al. (1961) interpreted these findings to mean that "productivity of the youngest producing age class reflects range conditions more sensitively than that of the older age classes". Their own work with mule deer shows that fertility of yearlings (the youngest producing age class) reflected range conditions better than fertility of older does and they present this as supporting evidence for their interpretation of the work done in New York. The fact that yearling fertility was not considered separately in either of the New York studies was apparently disregarded by Julander et al. (1961). My findings show that this probably is not justifiable. I was able to detect a significant difference ($P = .07$) in fertility between yearlings from the Duck and Turtle Mountains with a sample of 14 animals while this was not possible with a sample of 26 fawns although some fawns bred in each area. Apparently the youngest producing age class is not always the best indicator of range condition (although in the Whiteshell yearlings were both the best indicators of range condition and the youngest producing age class).

Prenatal Mortality

The significance of the two cases of fetal resorption found in Turtle Mountain does is unknown. Verme (1962) states that inadequate nutrition, particularly after mid-gestation, can result in mortality of fetuses. However, he also found prenatal mortality occurring in does on a high plane of nutrition. The does in which it was found in Turtle Mountain were in good physical condition and it is apparent that the fetal deaths did not result from inadequate maternal nutrition.

Breeding Among Female Fawns

The percentage of does that breed as fawns varies greatly with geographic location (Table 7) but literature on the subject indicates that range quality and not simple geographic location is the factor upon which fawn breeding depends. The absence of pregnant fawns from the Whiteshell and the relatively low pregnancy rates of Duck and Turtle Mountain fawns supposedly reflect low quality habitat. The significance of this is not clear since Table 8 shows very good fertility for adult does from all three Manitoba study areas. The picture is further complicated since comparisons of fawn size, as measured by overall length and length of hind foot, showed no obvious differences among the three areas (data were too limited and variable for statistical analysis) but it was noted that some Whiteshell fawns had attained greater physical dimensions than had some pregnant fawns from the other two areas. Apparently sufficient nutrients for growth were available to fawns from all areas but the additional requirements for sexual development were not available to Whiteshell fawns and were available to only a few fawns in the other two areas. But even in these areas it seems probable, since range quality is good, that only the most vigorous and well fed fawns can undergo estrus before growth and development are slowed by winter.

Although some fawns breed in the Duck and Turtle Mountains it is not known what contributions these deer make to population growth. It is well known that winter conditions are more severe on fawns than on older deer and this is especially so in the case of pregnant fawns. Therefore, more fetal deaths and immediate postnatal deaths of newborn fawns can be

Table 7. Regional variations in pregnancy rates of white-tailed deer fawns.

LOCATION	PREGNANCY RATE (%)	AUTHORITY
Northern New York	4	Morton and Cheatum (1946)
Southern New York	36	Morton and Cheatum (1946)
Massachusetts	60	Shaw and McLaughlin (1951)
Southern Texas	nil	Illige (1951)
Wisconsin	very low	Dahlberg and Guettinger (1956)
Missouri	26 to 74	Robb (1959)
Maine	25	Banasiak (1961)
Michigan	less than 10 to 60	Ryel and Fay (1961).
Iowa	75	Haugen and Trauger (1962)
Whiteshell	nil	see Fig. 3
Turtle Mountain	25	see Fig. 3
Duck Mountain	30	see Fig. 3

expected for deer that breed as fawns than for older deer. Since only about 25 percent of the fawns breed it is quite probable that they do not contribute greatly to population growth in average years.

A little-considered aspect of fawn breeding is the effect it may have on the future production of the individual. Nalbandov (1958) points out that reproductive efficiency seems to be an effect of previous reproductive performance and not of age. He cites a case in which female rabbits first bred at an early age had the same ovulation rate as females bred at 20 months. However, intra-uterine mortality during the second half of gestation among the does first bred at 20 months was much higher than for the early bred does. The older does produced an average of 3.6 young per litter while the earlier bred does averaged 5.5 young. This example suggests that reproductive efficiency of deer might also be affected by previous reproductive performance. Research on this subject might well reveal reproductive phenomena of use in explaining population growth patterns.

Significance of Condition Data

I concluded earlier that in my study areas some deer are lost yearly to malnutrition and many others are in poor physical condition. Apparently very few deer retain over 50 percent femur marrow fat until the end of the winter period and can be considered in "good" condition (using the standard given by Verme 1963). Verme (1962) found that if deer in "good" condition by mid-April are placed on a high nutritional plane they will lose less than 10 percent of their fawns and if deer in very poor condition by mid-April are placed on the same diet they will lose about 35 percent of their fawns. However, if deer in very poor condition are given restricted quantities of poor

food (just enough to keep them alive) they will lose over 90 percent of their fawns. Given a diet similar to that available to wild deer in non-agricultural areas they will lose about 50 percent of their fawns.

By comparing condition of deer from my study areas with condition levels of Verme's experimental deer I estimate that losses of newborn fawns will range from 20 to 50 percent in Manitoba following an "average" winter. Quality of the spring food supply apparently is very important and only in areas where deer supplement their natural diet with high quality agricultural crops can losses be expected to approach the minimum.

Fertility

Cowan and Wood (1955), speaking of "the growing conviction that the animal itself presents the most satisfactory measure of adequacy of the range upon which it has grown", stated "that it seems probable that only the animal is going to offer a satisfactory assessment of life conditions on any area." Since Cheatum and Severinghaus (1950) showed that fertility of white-tailed deer is dependent upon range quality, it is logical to assume that fertility is a good indicator of range adequacy. On this basis Table 8 shows that range and "life conditions" for yearling and adult deer from Turtle Mountain are among the best in North America. The high pregnancy and ovulation rates of adult does from Duck Mountain and the Whiteshell also indicate very good range; but the ovulation rates of yearlings appear to be considerably lower than for yearlings from States where adult ovulation rates are similar to rates for Whiteshell and Duck Mountain adults. The suggestion here seems to be that what constitutes good range and "life conditions" for adults is not necessarily so for yearlings. The fact that just as many fawns breed in Duck Mountain as

Table 8. Fertility of white-tailed deer from Manitoba compared to highest fertility levels reported from the United States (sample size in parentheses).

AREA	OVULATION RATE			PREGNANCY RATE		
	Fawns	Yearlings	Adults	Fawns	Yearlings	Adults
Maine ³⁾	1.38(18)	1.58(63)	1.79(71)	24.1(54)	80.8(78)	95.9(74)
Massachusetts ⁴⁾	1.06(10)	1.80(46)	2.04(85)	58.8(17)	92.0(50)	98.8(86)
West Virginia ⁵⁾	1 ¹⁾	1.77(84)	1.90(128)	n o t	g i v e n	
Iowa ⁶⁾	1.09(140)	2.15(66)	2.27(85)	n o t	g i v e n	
Michigan ⁷⁾	1.24(41) ²⁾	1.76(29)	1.93(42)	41.4(70)	100.0(29)	93.3(45)
Whiteshell		1.22(9)	1.92(36)	0.0(10)	90.0(10)	100.0(36)
Turtle Mountain	1.50(4)	2.00(7)	2.18(38)	25.0(16)	100.0(7)	97.5(33)
Duck Mountain	1.33(3)	1.43(7)	2.00(24)	30.0(10)	100.0(7)	100.0(24)

1) no data 2) fetal rates 3) Banasiak (1961) 4) Shaw and McLaughlin (1951) 5) Gill (1956)

6) Haugen and Trauger (1962) 7) Ryel and Fay (1961)

in Turtle Mountain (where range quality is excellent) shows that summer and autumn range conditions are very good in the Duck Mountain area, thus eliminating summer range as a factor causing low yearling fertility. This deduction leads to the conclusion that winter range or winter "life conditions" are responsible for lowering yearling fertility in Duck Mountain. This conclusion is supported by a similar one made by Pimlott (1959) concerning yearling moose and elk. Winter "life conditions" in the Whiteshell however, may not be the sole cause of lowered yearling fertility. Summer and autumn range conditions appear to be less than adequate there since no pregnant fawns were taken although the range is adequate to give good adult fertility and full growth expression.

Since Duck Mountain is considered to be underpopulated with deer it seems safe to say that the lowered fertility of yearlings is not primarily related to overpopulation. Apparently environmental resistance acting against fawns during their first winter is sufficient to result in lowered fertility (as yearlings) even though environmental resistance is not sufficient to materially offset adult fertility. The situation may be further aggravated by lowered quality of summer range.

The factors comprising environmental resistance are many and diverse but snow and low temperature are probably very important, as will be discussed later. Interspecific competition for food in Duck Mountain may also be a factor as moose and elk occupy range used by deer. Intraspecific competition must also be considered.

Interpretation of Results

I pointed out in my introductory remarks that deer management principles used in Manitoba have largely been adopted from the United States, especially the Lake States of Minnesota, Wisconsin and Michigan. This was in particular a reference to the idea that at least 20 percent of the autumn deer population must be harvested to prevent range damage and also to the idea that the food supply is the factor controlling deer numbers. The following discussion points out differences between Manitoba and Lake States environmental conditions that appear to warrant the adoption of a new deer management philosophy for Manitoba.

It has been made abundantly clear by Leopold (1943), Feeney (1943), Swift (1946), Leopold, Sows and Spencer (1947), Dahlberg and Guettinger (1956), Jenkins and Bartlett (1959) and Erickson et al. (1961) that closed seasons or inadequate harvests often lead to deer "irruptions" characterized by severely decreased fertility, decreased size, establishment of browse lines, destruction of preferred browse species and partial prevention of forest regeneration, and eventually culminate in mass die-offs due primarily to malnutrition. Since the Whiteshell study area has been almost unhunted for many years it is surprising that the population remains relatively stable and the range continues to be adequate. Evidently there are fundamental differences between the mechanisms controlling deer populations in the Whiteshell and in the Lake States where deer irruptions are well known. A very general discussion of Whiteshell and Lake States winter environmental conditions is sufficient to point this out. The divisions of environment are those proposed by Andrewartha and Birch (1954).

Weather

The following quotation from Bartlett (1950) effectively sums up the general thinking regarding the effects of temperature on white-tailed deer.

Normal temperatures occurring in the Upper Peninsula of Michigan are not critical for deer. While long periods of sub-zero weather are known to be detrimental to their welfare, even such occurrences are not necessarily critical if good winter food is plentiful and obtainable, and the deer are in good physical condition at the beginning of the cold period.

However, Darrow (1935) observed in New York that cold weather "seemed to pull deer down quite as much as wading through deep snow." Recently, experiments carried out at Cusino in Michigan's Upper Peninsula showed that pregnant white-tailed does fed nine common browse species ad libitum from early January to mid-April, lost 16 percent of their weight and femur marrow fat content was reduced to 50 to 70 percent by the end of the trial period (Verme 1962). This loss in condition can largely be attributed to increased energy requirements due to low temperatures and also to the tendency of deer to consume less food in winter even though it is available in abundance (French et al. 1956). While this decrease in condition was not critical for the experimental deer it is apparent that more severe environmental conditions could readily have reduced femur marrow fat reserves to dangerously low levels. Since the detrimental effects of temperature are more severe as temperature decreases it is not surprising that three of four deer collected in the Whiteshell in April 1963 were in critical condition, for data from Kendrew and Currie (1955) and

from the United States Weather Bureau show (Fig. 7) that winter temperatures at Winnipeg (near Whiteshell) are much more severe than at Chatham (near Cusino). This differential in winter temperatures is one of the major differences between Manitoba and the Lake States.

Snow acts to cover food and restrict deer movement and may thus exclude deer from portions of their range. These effects have long been realized as critical factors for deer in the Lake States and in the northeastern States. Severinghaus (1947) said of his work in New York: "in the Adirondack region, snow depth is the critical weather factor affecting winter mortality among deer . . .". It is evident from a discussion of Wisconsin winter range by Dahlberg and Guettinger (1956), that a similar situation exists in the Lake States. Because snowfall is considerably less in the Whiteshell, snow depth is probably of less importance there than in the Lake States. Over much of Michigan's Upper Peninsula, snowfall amounts to over 100 inches annually (United States Weather Bureau) while the Whiteshell average is 55 to 60 inches. The implications of this will be discussed later.

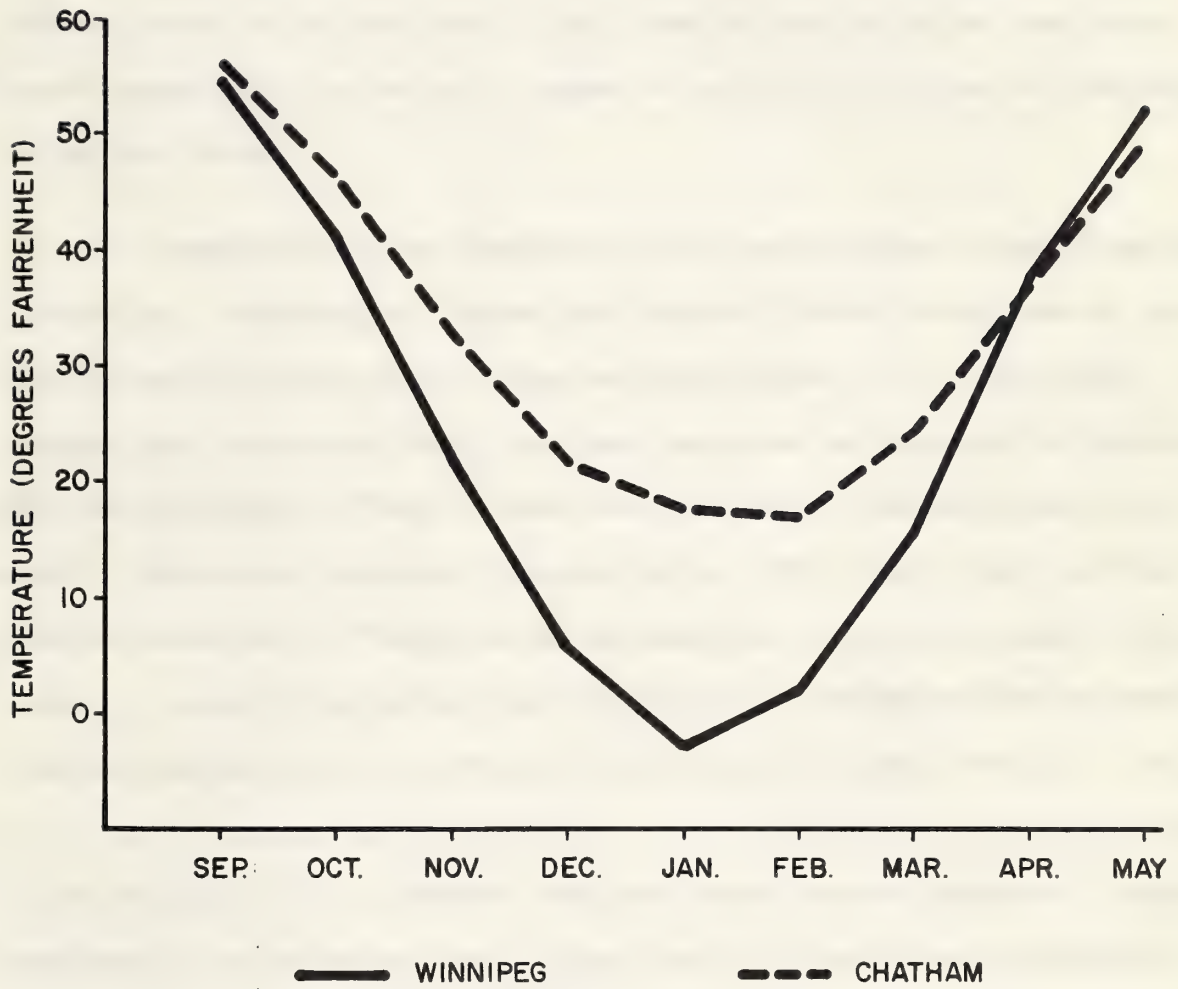
Food

The importance of the food supply was emphasized by Fowle (1950):

The environmental factor which has received the most attention in deer studies is food. Indeed, our concept of carrying capacity for deer centers around the adequacy of the food supply while our criteria of overuse have their basis in the rate of depletion of food supply.

Although it is impossible to compare directly the food supply per unit area in the Whiteshell with that in the Lake States it is important to

Fig. 7. Average monthly temperatures for Winnipeg (near Whiteshell) Manitoba and Chatham (near Cusino) Michigan.



point out that relatively more of the total food is available in the Whiteshell because of the lighter snowfall in that area.

Other animals and other organisms causing disease

Since quantitative information regarding predation and highway and railway deaths is not available it will have to suffice to say that these factors apparently are not major causes of mortality in either the Whiteshell or the Lake States.

Parasites are not considered to be a major direct cause of mortality in Michigan. According to Jenkins and Bartlett (1959), "no disease or parasite has made a serious dent in the deer population . . .". Similarly Dahlberg and Guettinger (1956) list many parasites and diseases of Wisconsin deer but state that: "None of them have ever caused serious losses in the state". Minnesota biologists (Erickson et al. 1961) take a more cautious view and state that: "Parasites and diseases are important natural causes of death. . . usually they affect deer indirectly, by weakening them and making them more susceptible to starvation, predation, and highway traffic". While it is fairly certain that parasites are not a major direct cause of mortality in the Whiteshell it is possible that even light loads of parasites, especially helminths of the digestive tract, might result in significant diversion of nutrients required by the host animal. Under severe winter environmental conditions losses due to malnutrition might be considerably increased. This point warrants further investigation.

The intensity of intraspecific competition for food among deer in the Whiteshell appears to be much lower than that encountered in many areas of the Lake States where competition has often progressed to such an extent

as to cause severely decreased weight and fertility and has several times led to deer die-offs during an irruption. My study has shown that these conditions do not exist in the Whiteshell nor are there records of such having ever occurred (although deer were apparently more numerous in the early 1940's than at present). However, the absence of these drastic effects does not mean the absence of competition. While there is no direct evidence for it among adults, the yearlings appear to suffer from competition during the winter. Pimlott (1959) concluded from his own work on moose and from literature reports that the level of nutrition during winter is the main factor controlling yearling breeding. Pimlott pointed out that Buechner and Swanson (1955) had found an increased percentage of pregnant yearling elk, following herd reduction, which they suggested was due to the same amount of food being utilized by fewer animals. Since Whiteshell range is entirely adequate to maintain high fertility in adult does (Table 8), it seems probable that reduced yearling fertility is not due to low range quality but is possibly due to the inability of fawns to compete with adults for preferred food plants during the winter.

I pointed out earlier that summer range in the Whiteshell may be less than adequate for yearlings and fawns of the year which also is indicative of intraspecific competition for food.

A place in which to live

Suitable places in which to live are often very limited for white-tailed deer during the winter months. In Michigan and Wisconsin such places only comprise 10 percent of the summer range (Bartlett 1950, Dahlberg and Guettinger 1956). These areas are the well-known deer yards that Swift (1946) defined as: "any continuous area where deer concentrate during a normal

winter". By this definition it must be said that deer in the Whiteshell yard up, but their "yards" occupy a much greater percentage of the summer range than do Lake States' yards. There are also great differences in deer density on winter range. According to Jenkins and Bartlett (1959) the Upper Peninsula of Michigan had an average of 30 deer per square mile in October 1956. This many deer (allowing for a 20 percent harvest) concentrated on 10 percent of the summer range during winter would mean an average of 240 deer per square mile. While I have no quantitative information on winter densities of Whiteshell deer I am quite sure that the average density does not exceed 10 deer per square mile.

The difference in yarding behaviour is apparently brought about by the snowfall differential between the Whiteshell and the Lake States. Swift (1946) speaking of the causes of yarding stated: "Cold weather does not determine it, but when the snow grows too deep, they will yard". Dahlberg and Guettinger (1956) found that deep snow causes deer to yard despite mild weather while low temperatures caused yarding to a much lesser degree. Banasiak (1961) reported that in Maine snow depth was important in restricting movement but it did not appear to be the primary cause of yarding as deer often congregated in yards before snow depth restricted travel. While there is not absolute agreement among these authors the general opinion seems to be that deep snow causes deer to yard while low temperatures either do not cause yarding or cause only very loose yarding. This I believe is a major key to understanding the population dynamics of Whiteshell deer.

Concluding Statements

I suggest that range destruction by deer does not occur in the

Whiteshell because each animal occupies a relatively much greater portion of its summer range during the winter than do deer in the Lake States. Range destruction and overbrowsing occur in the Lake States because snow confines deer to a small "place in which to live" thus causing them to utilize all available browse. The limited occurrences of overbrowsing observed in the Whiteshell are more often a result of deer choosing to heavily browse palatable species rather than being forced to browse any and all species in a given area just to keep alive.

The environmental resistance acting against Whiteshell deer is apparently so great in average winters that most deer are in poor condition by spring and a few apparently die in the face of an abundant food supply. Under such conditions the effects of competition for food are quickly felt if the population increases. The resulting decrease in fertility of the younger age classes and the increase in winter mortality combined with greater losses of newborn fawns are sufficient to stabilize the population before it irrupts.

The environmental resistance in this case comprises snow, cold, parasites, decreasing food quality and increasing dispersion due to competition, and even the threat of predators. None of these factors alone is sufficient to do the deer much harm but their combined effects result in a negative energy balance that leads to poor physical condition. Increased severity of any factor such as cold or competition results in a greater loss in condition with its attendant effects.

I concluded previously that lowered yearling fertility is not primarily due to overpopulation but it will be noted that I later used decreased

yearling fertility as an indicator of intraspecific competition for food. This apparent paradox arises from the use of two standards of overpopulation. The first denotes the human standard by which for example, six deer per square mile of habitat does not constitute an overpopulation. However, the second and more realistic way of assessing overpopulation is from the deer's point of view. Six deer in a group might constitute an overpopulation for the particular small area where they happen to be and in this manner competition would occur when other factors of the environmental resistance have already resulted in a serious negative energy balance. Any increase in group size or overlapping of group range would intensify this competition.

My interpretation has to this point been based upon information and observations from the Whiteshell area, but only because hunting is virtually absent there which means that all mortality is due to "natural" hazards. The effects of environment are in all probability similar in the Turtle and Duck Mountains although greater densities of deer can be carried in Turtle Mountain because of milder temperatures and greater quantity and better dispersion of food.

The mechanisms controlling deer populations in Manitoba allow a high level of fertility and because of this, high net productivity can be experienced periodically when winter environmental conditions are particularly favourable. For example, if the gross productivity of Turtle Mountain deer were realized, the autumn deer population would be approximately 50 percent fawns. Thus the long term carrying capacity could be far exceeded during a single favourable year but because these deer are not confined in yards where food is limited, there would probably not be a major die-off during the

following winter. But competition for food would be increased and this would lead to some increase in winter mortality and decrease in survival of newborn fawns. Under these circumstances it would take a number of years for the population to decrease to its former level in the absence of a severe winter or increased harvest.

It is also true that a particularly harsh winter can decimate a deer population under Manitoba conditions. The most recent such winter was experienced in 1955/56 and a large population decrease was the result. However, Leopold, Sows and Spencer (1947) made it very clear that such die-offs should not be confused with those resulting from a population irruption. Recovery from a winter die-off can be very rapid if followed by one or two very mild winters but is delayed by cold winters. It should be noted here that recovery following a die-off due to an irruption is always a slow process.

This study suggests that winter weather keeps the maximum density of deer in Manitoba at a level below that which the range can withstand. It also suggests that weather reduces net productivity, following an average winter, to a level below that realized by deer in the Lake States. These two phenomena are sufficient to invalidate the application of some Lake States management principles that have been used in Manitoba. If deer management is to be efficient in Manitoba it must be based upon research done in that Province.

RECOMMENDATIONS

1. Sex ratios and age class distribution of deer should be determined on one or two selected study areas for the purpose of calculating net productivity.
2. Concurrent with the first recommendation the relationship of winter weather to net productivity should be determined.
3. A general study of the ecology of deer during winter should be carried out in at least one representative area.

SUMMARY

1. Reproductive biology of white-tailed deer from three areas of Manitoba was studied during the winters of 1961, 1962 and 1963. In order of decreasing habitat quality they were the Turtle Mountain, Duck Mountain and Whiteshell areas. Altogether 99 adult, 24 yearling and 36 fawn does were collected for study.
2. Breeding activity reached a peak in November but Whiteshell deer bred significantly earlier than deer from the other areas. Photoperiod or temperature gradients did not adequately explain the difference. Nutritional or genetic factors may have been responsible.
3. Ovulation rates reflected habitat quality. Turtle Mountain adult does shed significantly more ova per doe than did Whiteshell adults. Yearlings from Turtle Mountain had an ovulation rate significantly higher than yearlings from the other two areas. Some Turtle and Duck Mountain fawns had ovulated but Whiteshell fawns had not.
4. Ovulation rate increased with age, reached a peak in 8½- and 9½-year-old deer and decreased slightly for older deer but differences between age groups older than yearlings were not statistically significant. Yearling and fawn ovulation rates were not significantly different but both were significantly lower than any adult age group. Fetal rates followed a similar pattern.
5. Adults from Turtle Mountain, Duck Mountain and Whiteshell lost 12.0, 4.5 and 1.5 percent of ova shed respectively. The high rate of loss suffered in Turtle Mountain was correlated with an increased frequency of triple ovulations as a result of a condition analogous to "flushing". Ova losses were

increasingly higher for yearlings and fawns compared to adults but samples were limited.

6. There were two fetal deaths in Turtle Mountain adults. Causes of deaths were not determined but it was noted that the does were in good physical condition.

7. Fetal rates for adult does from Turtle Mountain, Duck Mountain and Whiteshell were $1.92 \pm .09$ (38), $1.92 \pm .10$ (24) and $1.89 \pm .07$ (36). Yearling rates were $1.71 \pm .25$ (7), $1.29 \pm .18$ (7) and $1.11 \pm .11$ (9). The first yearling rate was significantly higher than the last two. Turtle Mountain fawns averaged $1.25 \pm .25$ (4) fetuses compared to $1.00 \pm .00$ (3) for Duck Mountain fawns.

8. The 1962 grouped ovulation rate of adult does from all areas was significantly lower than in 1961 or 1963. Fetal rates followed a similar but less pronounced pattern. The 1962 rate was significantly lower than 1961 only.

9. Fertility of yearling deer was more sensitive to changes in habitat quality than was fertility of adults or fawns.

10. Pregnancy rates in Turtle Mountain, Duck Mountain and the Whiteshell were 97.5, 100 and 100 percent for adults; 100, 100 and 90 percent for yearlings and 25, 30 and 0.0 percent for fawns. Rates for fawns are considered to be low compared to the very high pregnancy rates of older deer. It is suggested that the short summers in Manitoba may limit the number of fawns able to breed before winter slows their growth and development.

11. Length (minus tail) of adult does over 3 years of age from the

Whiteshell, Turtle Mountain and Duck Mountain measured 150.6 ± 1.26 (28), 149.6 ± 0.95 (39) and 144.4 ± 1.71 (20) cm respectively.

12. Three adult does with small button antlers were carrying apparently normal fetuses. There were no other anatomical peculiarities noted.

13. The observed fetal sex ratios varied slightly from area to area but did not depart significantly from a 100 to 100 ratio.

14. Measurement of the physical condition of deer during the final year of the study showed that some deer from all areas reached critical levels of malnutrition over winter despite an apparent abundance of food.

15. Fertility of adult does from all three study areas compared favourably with fertility levels reported for the species from several of the United States. Fertility of yearlings from Turtle Mountain also compared favourably but this was not the case for Duck Mountain and Whiteshell yearlings. Fertility of fawns from all areas appeared to be low relative to high adult fertility.

16. A general comparison of environment between the Whiteshell and the Lake States indicated that lighter snowfall in the Whiteshell allows deer to cover a greater part of their summer range during winter than do deer in the Lake States, but lower winter temperatures in the Whiteshell cause serious condition losses despite the availability of food. Under these circumstances intraspecific competition apparently occurs at low population levels and combined with the other factors comprising the environmental resistance, prevents deer irruptions and holds maximum deer density far below that of the Lake States. Similar mechanisms of population control are postulated for other areas of Manitoba.

17. The extreme importance of weather in the environmental resistance acting against deer in Manitoba is sufficient to invalidate the application of some deer management principles derived in areas where total food supply is the chief limiting factor.

18. It is concluded that the efficient management of deer in Manitoba can only be based upon research carried out under Manitoba environmental conditions.

LITERATURE CITED

- Adams, W. H. 1960. Population ecology of white-tailed deer in northeastern Alabama. *Ecology* 41:706-715.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago. 782 pp.
- Armstrong, Ruth A. 1950. Fetal development of the northern white-tailed deer (Odocoileus virginianus borealis Miller). *Am. Midland Naturalist* 43(3):650-666.
- Banasiak, C.F. 1961. Deer in Maine. Maine Game Div. Bull. 6. 159 pp.
- Bartlett, I. H. 1950. Michigan deer. Game Div., Michigan Dept. Conserv., Lansing. 50 pp.
- Bischoff, A. I. 1957. The breeding season of some California deer herds. *California Fish and Game* 43(1):91-96.
- Brohn, A., and D. Robb. 1955. Age composition, weights, and physical characteristics of Missouri's deer. *Missouri Conserv. Comm. Bull.* 13. 28 pp.
- Buechner, H. K., and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. *Trans. N. Am. Wildl. Conf.* 20:560-567.
- Cheatum, E. L. 1949a. The use of corpora lutea for determining ovulation incidence and variations in fertility of white-tailed deer. *Cornell Vet.* 39(3):282-291.
- . 1949b. Bone marrow as an index of malnutrition in deer. *New York State Conservationist.* 3(5):19-22.
- , and G. H. Morton. 1942. On occurrence of pregnancy in white-tailed deer fawns. *J. Mammal.* 23(2):210-211.

- Cheatum, E. L., and G. H. Morton. 1946. Breeding season of white-tailed deer in New York. *J. Wildl. Mgmt.* 10(3):249-263.
- , and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range conditions. *Trans. N. Am. Wildl. Conf.* 15: 170-190.
- Clegg, M. T., and W. F. Ganong. 1959. Environmental factors, other than nutrition, affecting reproduction, pp. 225-240. In H. H. Cole and P. T. Cupps, (ed.), *Reproduction in domestic animals*, Vol. 2. Academic Press, New York and London.
- Cowan, I. McT., and A. J. Wood. 1955. The growth rate of the black-tailed deer (Odocoileus hemionus columbianus). *J. Wildl. Mgmt.* 19(3):331-336.
- Dahlberg, B. L., and R. C. Guettinger. 1956. The white-tailed deer in Wisconsin. Wisconsin Conserv. Dept. Tech. Bull. 14. 282 pp.
- Darling, F. F. 1937. A herd of red deer. Oxford Univ. Press, London. 215 pp.
- Darrow, R. 1935. A study of the food preferences and requirements of the white-tailed deer in New York State. *Trans. Am. Game Conf.* 21:392-396.
- Erickson, A. B., V. E. Gunvalson, M. H. Stenlund, D. W. Burcalow, and L. H. Blankenship. 1961. Minnesota Dept. Conserv. Tech. Bull. 5. 64 pp.
- Feeney, W. S. 1943. Wisconsin deer today and tomorrow, pp. 12-19. In Wisconsin's deer problem. Wisconsin Conserv. Dept. Publ. 321.
- Fowle, C. D. 1950. The natural control of deer populations. *Proc. Ann. Conf. Intern. Game, Fish and Conserv. Comm.* 40:56-63.
- French, C. E., L. C. McEwen, N. D. Magruder, R. H. Ingram, and R. W. Swift. 1956. Nutrient requirements for growth and antler development in the white-tailed deer. *J. Wildl. Mgmt.* 20(3):221-232.
- Gibson, Doris. 1957. The ovary as an indicator of reproductive history in

- the white-tailed deer Odocoileus virginianus borealis, Miller. M.S. Thesis. Univ. Toronto, Toronto.
- Gill, J. 1956. Regional differences in size and productivity of deer in West Virginia. J. Wildl. Mgmt. 20(3):286-297.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America, Vol. 2. The Ronald Press Company, New York. 1083 pp.
- Harris, D. 1945. Symptoms of malnutrition in deer. J. Wildl. Mgmt. 9(4): 319-324.
- Haugen, A. O. 1963. An improved technique for preserving deer uteri. J. Wildl. Mgmt. 27(1):142-143.
- _____, and D. L. Trauger. 1962. Ovarian analysis for data on corpora lutea changes in white-tailed deer. Iowa Acad. Sci. 69:231-238.
- Illige, D. 1951. An analysis of the reproductive pattern of whitetail deer in south Texas. J. Mammal. 32(4):411-421.
- Jenkins, D. H., and I. H. Bartlett. 1959. Michigan whitetails. Game Div., Michigan Dept. Conserv., Lansing. 80 pp.
- Julander, O., W. L. Robinette, and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. J. Wildl. Mgmt. 25(1): 54-60.
- Kellogg, R. 1956. What and where are the whitetails, pp. 31-55. In W. P. Taylor, (ed.), The deer of North America. The Stackpole Co., Harrisburg.
- Kendrew, W. G., and B. W. Currie. 1955. The climate of central Canada. Queen's Printer, Ottawa. 194 pp.
- Krumholz, L. A., R. W. Darrow, O. H. Hewitt, and E. L. Kozicky. 1957. Glossary of wildlife terms. J. Wildl. Mgmt. 21(3):373-376.
- Leopold, A. 1943. Deer irruptions, pp. 1-11. In Wisconsin's deer problem. Wisconsin Conserv. Dept. Publ. 321.

- Leopold, A., L. K. Sows, and D. L. Spencer. 1947. A survey of over-populated deer ranges in the United States. *J. Wildl. Mgmt.* 11(2):162-177.
- Loveless, C. M. 1959. The Everglades deer herd life history and management. Florida Game and Fresh Water Fish Comm. Tech. Bull. 6. 104 pp.
- Low, W. A., and I. McT. Cowan. 1963. Age determination of deer by annular structure of dental cement. *J. Wildl. Mgmt.* 27(3):466-471.
- Manitoba Department of Industry and Commerce. 1960. Economic atlas of Manitoba. Winnipeg. 81 pp.
- McCabe, R. A., and A. S. Leopold. 1951. Breeding season of the Sonora white-tailed deer. *J. Wildl. Mgmt.* 15(4):433-434.
- McEwan, E. H. 1963. Seasonal annuli in the cementum of the teeth of barren ground caribou. *Can. J. Zool.* 41:111-113.
- Mitchell, B. 1963. Determination of age in Scottish red deer from growth layers in dental cement. *Nature* 198(4878):350-351.
- Morton, G. H., and E. L. Cheatum. 1946. Regional differences in breeding potential of white-tailed deer in New York. *J. Wildl. Mgmt.* 10(3):242-248.
- Moustgaard, J. 1959. Nutrition and reproduction in domestic animals, pp. 169-223. In H. H. Cole and P. T. Cupps, (ed.), *Reproduction in domestic animals*, Vol. 2. Academic Press, New York and London.
- Nalbandov, A. V. 1958. Reproductive physiology. W. H. Freeman and Co., San Francisco and London. 271 pp.
- Noble, R. E. 1960. Progress report on white-tailed deer productivity studies in Mississippi. *S. E. Assoc. Game and Fish Comm. Meeting* 14:53-60.
- Pimlott, D. H. 1959. Reproduction and productivity of Newfoundland moose. *J. Wildl. Mgmt.* 23(4):381-401.
- , and H. W. Mossman. 1959. A macroscopic ovary sectioning method. *J. Wildl. Mgmt.* 23(2):232-233.

- Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. *New Zealand J. Sci. Technol.* 36(5):429-463.
- Robb, D. 1959. Missouri's deer herd. Missouri Conserv. Comm., Jefferson City. 44 pp.
- Robinette, W. L., J. S. Gashwiler, D. A. Jones, and H. S. Crane. 1955. Fertility of mule deer in Utah. *J. Wildl. Mgmt.* 19(1):115-136.
- Ruhl, H. D. 1956. Hunting the whitetail, pp. 261-331. In W. P. Taylor, (ed.), the deer of North America. The Stackpole Co., Harrisburg.
- Ryel, L. A., and L. D. Fay. 1961. Deer biological data 1960-61. Michigan Dept. Conserv. Rept. 2344. 25 pp.
- Sergeant, D. E., and D. H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. *J. Wildl. Mgmt.* 23(3):315-321.
- Severinghaus, C. W. 1947. Relationship of weather to winter mortality and population levels among deer in the Adirondack region of New York. *Trans. N. Am. Wildl. Conf.* 12:212-223.
- . 1949. Tooth development and wear as criteria of age in white-tailed deer. *J. Wildl. Mgmt.* 13(2):195-216.
- . 1951. A study of productivity and mortality of corralled deer. *J. Wildl. Mgmt.* 15(1):73-80.
- , and E. L. Cheatum. 1956. The life and times of the white-tailed deer, pp. 57-186. In W. P. Taylor, (ed.), The deer of North America. The Stackpole Co., Harrisburg.
- Shaw, S. P., and C. L. McLaughlin. 1951. The management of white-tailed deer in Massachusetts. Massachusetts Div. Fisheries and Game Res. Bull. 13. 59 pp.

Simpson, G. G., Anne Roe, and R. C. Lewontin. 1960. Quantitative zoology.

Rev. ed. Harcourt, Brace and Co., New York. 440 pp.

Swift, E. 1946. A history of Wisconsin deer. Wisconsin Conserv. Dept. Publ.

323. 96 pp.

United States Weather Bureau. Climatography of the United States No. 11-16.

U. S. Government Printing Office, Washington. 56 pp.

Verme, L. J. 1962. Mortality of white-tailed deer fawns in relation to

nutrition. Proc. 1st Natl. White-tailed Deer Disease Symposium. Univ.

Georgia, Athens. 1:15-28.

———. 1963. Effect of nutrition on growth of white-tailed deer fawns.

Trans. N. Am. Wildl. Conf. 28:431-442.

B29818